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AN HISTORICAL SURVEY OF VESTIBULAR EQUILIBRATION

by

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FOREWORD

The historical task undertaken in this volume was incited by the problem of bodily equilibration in flight, a problem which aroused widespread interest during the World War. After we entered the War, a small group of American psychologists, temporarily attached to the Federal Air Service, came by way of experiment upon novel facts regarding the mode of operation of the auditory vestibule and canals and the probable significance of these organs in the maintenance of bodily balance and adjustment. These facts stood at such wide variance from current otological practices and traditions that it seemed advisable to institute new experimental researches and also to set the whole problem of equilibration in clear historical perspective. The sketch which follows has been written in connection with one group of these researches, the group carried out at the psychological laboratories at the University of Illinois. It is the author's hope that the historical sketch and the bibliographical references which accompany it may be of use both in subsequent investigations and also in applying the results of research to the problems of flight, in the practice of medicine, and elsewhere.

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AN HISTORICAL SURVEY OF VESTIBULAR EQUILIBRATION

COLEMAN R. GRIFFITH, Ph.D.

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I.

INTRODUCTION

WHEN, in 1825, Flourens first demonstrated the fact that certain effects of cerebellar excitation could be duplicated by disturbing definite portions of the internal ear,—the semicircular canals,—an experimental program of no mean dimensions was set for the sciences of life. It had commonly been supposed that the whole of the internal ear was solely concerned with audition; but here was a demonstration that suggested the existence of close functional relations between the ear and the cerebellum and, therefore, between the ear and the entire musculature of the body. As a result, a comprehensive plan of investigation was outlined, and the succeeding decades brought forth an imposing number of experimental papers upon the structure and the functions of the semicircular canals. These empirical studies form a brilliant chapter in the history of the biological sciences, not only as regards the discovery of new facts but brilliant also in its new technique and in its invention of novel methods.

But Flourens' demonstration further suggested a psychological problem of considerable importance. Purkinje had already described with great fidelity the behavior of objects in the visual field subsequent to rotation. It was soon pointed out, moreover, that the visual field was similarly disturbed when the semicircular canals were excited in the manner suggested by Flourens. These facts were further related to observations upon dizziness and vertigo, and thus they suggested a description, under experiment, of the profound modifications of mind brought about by stimulation of the alleged 'non-acoustical' part of the ear.

II

THE PROBLEMS

NOW a cursory survey of the literature since Flourens reveals a number of specific problems. It is our present task to distinguish these problems, to describe them in detail, together with the relevant experimental evidence, and finally to come to a general statement of the significance of the whole survey. The problems which we shall distinguish are: (A) the isolation of a new receptor, (B) the structure of this receptor, (C) its mode of excitation, (D) the theories of vestibular function, (E) the central connections of the receptor, (F) the history of the receptor, (G) recent clinical methods and results, and (H) the psychologist's analysis and description of the gross experience of dizziness and of disequilibration.

A. The Isolation of a New Receptor.

The experimental isolation of a new receptor sensitive to disturbances of equilibrium was a long task. As we have intimated, the first step proved the similarity between the behavior excited by the stimulation of the semicircular canals, that excited by the stimulation of the cerebellum or of one branch of the VIIIth nerve, and that aroused by whirling on the heel or arising suddenly from a reclining position. This observed similarity was used by a number of investigators to establish the doctrine that the non-acoustical portion of the ear was the sole receptor for the maintenance of equilibrium. Others adhered to a more conservative position, holding that the canals were not the only organs of bodily balance. And again, a third group of writers continued to deny all equilibratory function to the canals, some of them assigning to these structures an entirely different function.

1. *The development of adequate experimental methods.* The experimental investigation of the better known sense organs has been materially aided by the fact that for each of them there is an adequate stimulus, or a stimulus to which they are specifically tuned. As a general rule, these sense organs show wide differences between the effects induced by the adequate stimulus and those induced by stimuli

that are but partially adequate. The experimental attack upon a possible end-organ of equilibration has, however, benefited from no such relation between stimuli and psychosomatic events. As a matter of fact, the numerous physical conditions under which disturbances of equilibrium can be produced have been a serious hindrance to the successful development of experimental methods. There are no less than six different conditions which may issue in disturbances of balance. Rotation or translation of the body, electrical contacts near the ear, warm or cold water or air within the meatus, cutting or extirpating the semicircular canals, the eighth nerve or parts of the cerebellum, pressure upon the ear drum, or anaesthetizing or cocainizing the ear, all issue in about the same general kind of disturbance. The physical conditions we have named have been fairly well described during the course of aural research and we may speak, therefore, of (1) the method of rotation, (2) the galvanic methods, (3) the thermal methods, (4) the surgical methods, (5) the compression methods and (6) the chemical methods.

The method of rotation had its beginning, apparently, in the hands of Purkinje (*1257*) and almost every investigator since his time has used it in one form or another. The method was greatly improved and extended by Mach (*1015*, *1016*) and in the hands of Boeters (*248*), Bondy (*252*), Buys (*364*, *369-373*, *375-376*), Cassirer and Laeser (*398*), Hesse (*764*), Lombard and Balderweck (*992*), Mackenzie (*1028*, *1030*), Neumann (*1172*), Piéron (*1229*), Schäfer, (*1371*, *1372*), Wittmaack (*1654*), and Wojatschek (*1664-1667*), notable additions have been made regarding the functions of the semicircular canals. Bárány (*96*, *98*, *100*) adapted the method to the clinical laboratory. The most serious quantitative changes in the method were made at the Mineola Research Laboratory (*1054*), changes which Griffith (*649-699*) adopted and found extremely valuable.[1]

The galvanic method has likewise had a long history, the early stages of which are suggested by such names as Purkinje (*1259*, p. 297), Ritter (*1315*), Remak (*1295*), Benedikt (*198*, *199*), Brenner (*309*), Breuer (*315*), Hitzig (*769*), Jensen (*827*) and Kny (*880*).

[1]The method of rotation in an extreme form has been used to centrifuge developing eggs and other structures. The results of such procedures are still in doubt but the method may be significant when applied to the canals. See Clement (*418*), Conklin (*426*), Hertwig (*758*, *759*), Morgan (*1130*), Moskowski (*1135*), Pflüger (*1222*, *1223*), Stein (*1467*, *1474*), and Wetzel (*1625*).

Of these investigators, Hitzig (*op. cit.*, p. 716 ff.) was the first to give a clear and accurate account of "galvanic vertigo." Others who have used the method to advantage are Babinski (*73-78*), Blau (*242, 243*), Buys and Hennebert (*378, 379*), Dyrenfurth (*545*), Katolinsky (*851*), Kuffler (*918*), Mackenzie (*1023, 1029*), Mann (*1050-1052*), Marx (*1072-1074*), Strehl (*1514*), Urbantschitsch (*1576*) and Zalewski (*1689*). Jones (*839*, pp. 247 ff.) has made a recent evaluation of the method.

The origin and early history of the caloric or thermal method is not so clear, although Goltz (*667*) said in 1870 that the effects of the use of hot and cold water had become common knowledge by that time. The method has made use not only of cold and warm water, but of cold and warm air and of observations upon individuals suffering under high fevers. Baginsky (*83*), Bornhardt (*285, 286*), Hofer (*775-777*), Kallman (*847*), Kubo (*916*), Lucal (*998*), Schwartze (*1396*), Spamer (*1444*) and Urbantschitsch (*1575*) all found ocular and head movements after cold and warm water stimulation. Hitzig (*769*) also observed the effects of caloric excitation; although he apparently failed to see the relation between the facts obtained by this method and those obtained by means of the galvanic method. Other studies based upon the thermal methods were made by Boeters (*248*), Davranches (*490, 491*), Fowler (*604*), Grain (*679*), Grant (*680, 681*), Hesse (*764*), Mach (*1140*), Popp (*1245*), Quix (*1270*), Rosenfeld (*1323, 1324*), and Zalewski (*1689, 1690.*)

Beginning with Flourens the surgical method has been the most widely used of all the methods for exciting the canals. The method includes every form of cutting, of pricking or puncturing, and of extirpating either the canals, the vestibular branch of the VIIIth nerve, or the functionally related parts of the cerebellum. Although almost every investigator of the 80's and 90's used the surgical method, a few were inclined to give it special attention. Among them may be mentioned Böttscher (*293*), Bourdan (*294*), Bontau (*300*), Camis (*387*), Kleijn (*870*), Mingazzini and Polimanti (*1119*), Stenger (*1486*), Stein (*1459*) and Trendelenberg (*1544*).

Alexander (*27, 28*), Lucae (*998*) and Mygind (*1162*) observed that pressure caused the ocular twitchings known as nystagmus.[2] Alexander laid claim to the first use of the method of pressure; but Bárány (see Alexander *27*, p. 91) corrects him by citing several of the

[2]See also Goltz (*667*, p. 192).

investigators who had already observed the effects of mechanical force. Other investigators to note and use the method of compression are Blake (*240*), Jackson (*819*), Morisset (*1137*), and Stein (*1473*). Although Baginsky (*84*) found the same results, he ascribed them to pressure on the brain; but Höyges (*789*, p. 558) and Spamer (*1444*, p. 177) have denied this possibility. Thomas and Egger (*1532*), finally, have studied the effects of compression on the VIIIth nerve. We shall not speak at this time of pathological cases in which pressures have been exerted on various parts of the equilibratory mechanism.

Gaglio (*637–640*) obtained the same results in anaesthetizing the canals as others had obtained by injuring them. The chemical means of attacking the semicircular canals are, however, about as unsatisfactory as are the compression methods. Of scattered papers making use of the method, those by Copaldo (*428*), Goldman (*661*) and Strumpell (*1517*) make use of etherization while König (*891*) cocainized the canals. A number of other chemicals are also known to lead to aural excitation of the kind we are considering.

2. *Demonstration of the similarity of responses to ampullar and to cerebellar excitation.* Scientific descriptions of the functions of the cerebellum began, apparently, with Rolando[3] (See Thomas, *1528*); although Petit is said to have made, a little earlier, some rather crude experiments upon the same structure.[4] The experimental investigations which were to lead to a definite distinction between vestibular and auditory functions began, however, with Scarpa, who, in 1769, gave the first description of the vestibular ganglion and of its relation to the cerebellum (see Scott, *1399*, p. 1601), although Sherrington (*1422*, p. 894; *1424*) refers to du Verney as making, in 1697, the first experiments on ablation of the cerebellum with the notation that there still remained some "use of sense."[5] About

[3]See Rolando,—., Saggio sopra la vera struttura del cervello e sopra le funzioni del sistema nervoso. Sassari, 1809. Zweite Ausgabe, Turin, 1828.

[4]Literature regarding the ear as an end-organ for hearing runs back quite as far. See, for example, Duverney (*542, 543, 544*), Geoffroy (*651*), Mathesius (*1081*), Meckel (*1107*), and others.

[5]Du Verney is also mentioned as writing in 1727 (published after his death) the first special treatise on aural disease in the English language. (Wilde, *1629*, p. 15). Wilde (pp. 1-50) has also given an account of all aural investigations up to his time. He begins, for example, with the first special work to be written on the ear, *viz.*, Mercurialis, H., De oculorum et aurium affectibus praelectiones, Frankfort, 1584. Wilde seems not to have known of the possible equilibratory functions of the ear; although he speaks (pp. 371 ff.) of cases of violent convulsions resulting from aural puncture or from disease. Later, however, he speaks of the whole inner ear as being concerned with hearing. (p. 373).

1820, Purkinje (*1257*, *1258*, *1259*) described in detail the experiences resulting from rotation about a vertical axis, attributing them to certain changes in the head; but Erasmus Darwin (*488*) had, as early as 1795, made many similar observations without, however, suggesting any special sense-organs. A few years later, Autenrieth (*64*) had considered the canals as a possible means for the perception of the direction of sound, while Gruithausen (*703*) attributed (in 1810) the perception of all active and passive movements of the body to an alleged "muscle sense."

To Flourens, however, must be given the honor of having done the first systematic work on the mechanisms of equilibration. His studies were, in fact, so outstanding and so epoch-making in the history of vestibular functions, that they have influenced the course of research up to the present time.[6] In 1824 he reported experiments from which he concluded that injury to the semicircular canals of animals caused such motor incoordination as unusual movements of the eyes and also definite disturbances of equilibrium, all of which were quite comparable to the facts described by Purkinje as appearing under other conditions. "Je retranchai le cervelet d'un autre pigeon. Arrivé aux couches moyennes, je touchai la moelle alongée, et il y eut un trémoussement convulsif. Ce trémoussement dissipé, je continnai mon opération. Les mouvements désordonnés et impétueux reparurent aux mêmes couches que dans l'expérience précédente. L'animal perdit de même la faculté de se tenir en équilibre, de marcher et de voler; it était dans une agitation presque continuelle; il voulait et se mouvait, mais il ne se mouvait jamais comme il le voulait."[7]

The more elaborate report of these and of other experiments, made some years later (*602*), has become classical in the history of the subject. By extirpating portions of the canals and of the cerebelli of pigeons, he not only verified the fact that equilibratory disturbances were excited by injury to the deep structures of the cerebellum but he definitely concluded that the same thing occurred with injury to the semicircular canals alone (*602*, pp. 438-501). His work was analytical enough,—early and pioneering as it was,—to demon-

[6]Over fifty years later, when the experimental problems were most numerous, as a result of the impetus given by Flourens, Crum Brown magnifies him by saying that "his experiments were conducted with an amount of care and the results described with a degree of accuracy and clearness not surpassed by any recent investigator." (*442*, p. 634).

[7]See Flourens, *599*, p. 37; also *600*, *601*, *602*.

strate that the section of a membranous canal was always followed by movements of the head or even of the body of the animal in the direction of the divided canal; more precisely, by oscillatory movements of rotation about an axis at right angles to the plane of the divided canal.[8]. This observation agrees with those made by Darwin (*488*) and by Purkinje (*1258*) who had noticed that the position of the imaginary axis of apparent rotation for external objects depended upon the axis of rotation executed at the head; and that, if the position of the head were changed after having arrested the movement of the body, the axis of imaginary rotation was found to remain unaltered.[9] Flourens also showed that the movements were much more violent and that the loss of equilibrium was much more persistent when the corresponding canals of both sides were cut than when one only, or when two dissimilar canals were divided; and that when all six canals were destroyed violent and complex convulsions continued for several days. If the animal survived this stage, it gradually attained a condition in which its movements were effected with great deliberation, and in which the sense of sight was absolutely necessary to the creature's self-direction.[10]

3. *Experimental evidence for a new receptor.* The belief that the ear served no other purpose than that of audition was so strongly rooted, however, that practically thirty years passed before the subject again became one of popular interest. Nevertheless, the work of Flourens had served definitely to establish the similarity between the behavior resulting from violation of the cerebellum, that resulting from excitation of the semicircular canals, and that described by Purkinje.[11] Even though several investigators believed

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[8]Chevreul (*407*) was the first of several investigators to contend that the disturbances resulting from the Flourens' experiments were inhibitory and not excitatory as Flourens contended. This view did not long prevail.

[9]See *1166*, pp. 764-765.

[10]Numerous observers have reported the course of the recovery that takes place in animals after surgical means of exciting the canals have been resorted to. In most cases the recovery (indicated by the disappearance of unusual movements) has been far more rapid than the healing of the wound. It is curious that this fact did not suggest that continued excitation of the canals (which in the case of a wound to the canals would seem to be the case) might lead to a profound modification of the effects of ampullar stimulation. As the facts stand, almost if not quite all the observations that have been made rest upon the immediate effects of vestibular excitation, a circumstance which has, apparently, distorted the whole history of labyrinthine function. Recent experiments go to show that repeated stimulation of the equilibratory mechanisms results in important functional modifications.

[11]As a matter of fact, as late as 1887 Ewald (*557*) was unable to distinguish clearly between the functions of the cerebellum and those of the semicircular canals.

that Flourens' experiments on the ear had also involved cerebellar destruction, the problem was set, and, subsequent to 1860, a host of researches appeared, some confirming and some denying the existence of a new receptor.

There are, in fact, several reasons why the experimental data should be at variance. (a) In the first place, the canals are exceedingly small and they stand, moreover, in close anatomical and functional relations with the cerebellum.[12] Under these conditions, it was a task to discover whether identical surgical procedures had at all accomplished the same results.[13] (b) In the second place, the locus of chief effect of excitation of the canals varies from organism to organism. Frequently, certain ocular movements are the only visible sign of disturbance and in some other forms even these movements may be so small as to escape detection.

As a matter of fact, at least five specific kinds of response have been referred to the semicircular canals. The ocular movements, a rhythmic jerking to and fro or in circular fashion, depending upon the character of the stimulus, are known as "vestibular nystagmus" and have been used most frequently for observation. Loeb (*991*), Stevenson (*1496*) and Urbantschitsch (*1577*), have described similar movements of the head or "head nystagmus," while Wodak (*1662*) has discovered a vestibular pupillary reflex. Other somatic disturbances belong either to the gross musculature or to the vascular, digestive, and respiratory systems. In the first case, extensions and flexions of the limbs result and in the second, a variety of vascular and digestive disturbances ensue.

Furthermore, it has been shown elsewhere (*694-699*) that all the results of rotation are highly sensitive to the conditions under which they appear. It is obvious, for example, that controlled stimulation by surgical means is a difficult matter and, as we know, most of the early work was of this nature. (c) Again, it has been demonstrated that all the effects of ampullar stimulation are highly modifiable under repetition,—even by limited repetition in some cases (*694-699*). Some experimenters have taken account only of the initial effects of disturbing the canals while others have studied the later effects, assuming that a surgical violation of the canals provided a source of

[12] See Baginsky (*85*) and Russell (*1347*, p. 427).
[13] See Lange, (*942*, p. 615), and Wilson and Pike, (*1639*, p. 913)

excitation continuing as long as the wound was unhealed. (d) Finally, we are not yet able to state just where the essential end-organs for equilibrium lie. The contention of Loeb (*989*) and others, and more recently of Maxwell (*1092*, *1093*, *1094*) that the otoliths are really the end-organs concerned in equilibrium, while the canals are but a means of equalizing the pressure (Maxwell), suggests that while different investigators have noted different effects, their results need not be considered contradictory but as calling for a further refinement of method.

With these things in mind we shall proceed to state the facts as we have found them. Harless (*724*) and Czermak (*481*) confirmed Flourens' experiments. Brown-Séquard (*331*) operated on frogs and rabbits and found equilibratory disturbances continuing for some time. Vulpian (*1615*) found motor disturbances after sectioning the canals, and about the same time Toynbee (*1511*) described the disappearance of vertigo following pathological exudation of the internal ear. A year later Carville (*397*) noted violent head-movements which became pendular when the canals were disturbed. Still more important were the investigations of Löwenberg (*995-996*), who proved conclusively that disturbances of balance were not due to an injured cerebellum. This observation has been well substantiated in spite of the apparent demonstration of Baginsky (*84*) and Quincke (*1263*) and others that the cerebro-spinal fluid is disturbed whenever the fluid in the canals is disturbed. Höyges (*789*), however, passed a tube into a rabbit so as to take out the cerebro-spinal fluid and found no evidence of equilibratory disturbances. Löwenberg (995–996) cut and otherwise excited the canals of birds and found that the lack of muscular coordination was due, not to paralysis, but to excitation, and that the excited movements were reflex and unconscious.

Within a short time the technique of stimulating and extirpating the minute canals was so perfected as to become in the hands of Ewald (*562*), Cyon (*455*), and others, a means to very delicate operations and precise and dependable results. Mechanical contrivances of a really clever sort were constructed in order to illustrate the possible mechanism (*444*). Nagel (*1166*, p. 792) describes an instrument used for many years at Freiberg in the schematic representation of the vestibular mechanism, while Mach (*1020*, pp. 74 ff.)

specifies an instrument which he devised for the purpose of observing the behavior of small animals under rotation at high speed.[14]

Although the evidence supporting the existence of a new receptor was all circumstantial, it involved, nevertheless, many animal forms, various methods of excitation,—surgical, galvanic, chemical, rotational, mechanical and thermal,—as well as deductions from the phylogenetic and ontogenetic history of the ear. Spamer (*1442*, *1443*, *1444*), using several of these methods, made an unusually elaborate study of the canals, and concluded therefrom that the canals were peripheral organs "für das Gleichgewichtsgefühl, den 'Statischen Sinn' (Breuer) und bezw. die Coordination der Bewegungen darstellen."[15] Delage (*499*, *500*) and Aubert (*58*, *59*, *60*), working on human subjects, Goltz (*667*) using doves, Hasse (*730*), Hensen (*750*)[16], Schrader (*1391*, *1392*) and Schklarewsky (*1384*, *1385*), working on birds and frogs, Frölich (*632*) working on the sea-horse, Sewall (*1406*) on sharks, and Loeb (*988*) on the dogfish, found that definite disturbances resulted when certain portions of the ear were violated. In the case of animals, these effects were either movements of the head in the plane of the divided canal or peculiarities of movements after recovery. Berthold (*213*) and Bornhardt (*285*, *286*, *287*) found that disturbances of the perilymph in pigeons resulted in instability, while pressure and suction on the canals induced a pendular movement of the head. Berthold (*213*), furthermore, as well as Sewall (*1406*), confirmed the reflex nature of canal function as first indicated by Löwenberg. Matte (*1082*, *1083*, *1085*) and Bernstein (*211*) also concluded that the canals were equilibratory in function. Exner (*572*) observed that aural suppuration produced disturbances of the same kind as cutting the canals, while Budge (*357*) related vertigo to movements of the perilymph. Michalski (*1114*) cut the canals of doves and also used chemical and galvanic stimuli with positive result. Similar conclusions were reached by Schwartze (*1396*), Munk (*1147*), Brücke (*335a*), Loeb (*990*), Bethe (*216*, *217*), Henri (*747*), Beer (*190*, *191*), and Schwabach (*1394*).

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[14]See also Alexander (*26*), Delage (*505*), Fridenberg (*617*, *618*), and Grant (*681*, *682*.)

[15]The writer has been unable to determine just when and where a distinction was ever made between the canals as end-organs and the ampullar fibrils within the canals as end-organs. It has been customary to speak of the canals when the ampullar endings must have been meant and we shall, accordingly, speak of the canals in the same manner.

[16]Hensen, however, believed the canals to be essentially acoustic in function. See Hensen (*751*).

James' historic experiment (*822*) on deaf-mutes, in some of whom the canals were affected, did much to establish the relation between equilibrium and these organs. His argument rested on the fact that since a certain proportion of deaf-mutes lost their equilibrium under water and in the dark and that a similar proportion were later found to have defective canals, it was not unreasonable to suppose that some relation existed between the canals and the maintenance of equilibrium. James' results were confirmed in the clinical laboratory by Buck (*352*). More recently, as we shall see, the clinical laboratory has furnished a good deal of material of this kind. (Cf. below, pp. 46 ff.). Crum Brown (*442*, p. 658), curiously enough, had already seen (in 1878) the need of work like James' and of other clinical observations. He says: "A great deal of valuable information might be obtained by carefully testing the delicacy and accuracy of the sense of rotation in deaf-mutes. Many deaf-mutes have not only the cochlea, but the whole internal ear, destroyed; if then, the inmates of deaf and dumb establishments were systematically tested by means of such experiments as Mach and Brown made upon themselves and if the condition of the internal ear were, in each case of *postmortem* examination of a deaf-mute, accurately noted, we should soon obtain a mass of information which would do more to clear up the relation between the sense of rotation and the semicircular canals than any number of experiments on animals unable to describe to us their sensations." As a matter of fact, James' work has given rise to a considerable literature on the subject. At Breuer's suggestion, Kreidl (*903*) repeated the experiments and came to the conclusion that the semicircular canals were "static senses" since about the same number of deaf-mutes were deficient in equilibratory powers as later proved to have deficient canals. Alexander and Bárány (*34*), Alexander and MacKenzie (*43*), Alexander and Kreidl (*41*), Bach (*82*), Brock (*327*), Bruck (*335*), Doehne (*526*), Frey and Hammerschlag (*614*, *615*), Kano (*848*, *849*), Mygind (*1158*, *1159*), Pollak (*1244*), Stern (*1492*), Strehl (*1513*), Tweedie (*1565*) and Wanner (*1609*) have made similar studies upon the deaf and upon deaf-mutes and have come, for the most part, to the same conclusions.

Ewald (*561*, *562*, *563*) found that, with one labyrinth gone, the frog, when swimming, moved with one side of the body lower in the water than the other. The contralateral fore-limb was extended, *i. e.*, unilateral ablation of the labyrinth in the frog caused ipsolateral

flexions and contralateral extensions of the head and limbs. He also investigated muscular tone and found weakness in the limbs of the contralateral side. He was able, furthermore, to point out a definite relation between the intensity of stimulation and the resulting effects, either in the same animal or in different animals (*557*, p. 481). Emmanuel (*582*) described corroborative changes in muscle curves in frogs. Van Rossem (*1327*) found that unilateral ablation of the labyrinth in the tortoise caused ipsolateral flexion and contralteral extension of the head and limb. Lee's classical work (*957*, *958*) on the sense of equilibrium in fishes has done much to confirm the relation of the canals to equilibrium, all of his results testifying to the belief that the vestibular portions of the ear were the chief organs of equilibrium. In 1898 (*959*) he decided that certain morphological facts proved conclusively that the ear and the lateral line organs are phylogenetically the same, thus introducing genetic evidence that the ear may be, in part, equilibratory in function,—a result confirming the work of Fuchs (*633*). Lee found that both organs develop from the same ectodermal thickening. Bonnier (*263*) has shown that fishes whose lateral organs had been destroyed by galvano-cautery largely lost the capacity of correct orientation during disturbances of the water. Lyon (*1011*, *1012*) did two studies most faithfully and concluded that the canals are a specific endorgan of equilibration. Maxwell (*1090*, *1091*), working on sharks and Wilson and Pike (*1635*, *1636*, *1637*) working on the dog and upon turtles confirmed in a careful manner the equilibratory functions of the canals. Maxwell discovered the existence of a "torsion effect" as the actual cause of the disturbances found.

Streeter (*1505*, *1506*, *1507*) turned from adult to immature forms. By comparing the behavior of normal tadpoles with that of tadpoles from whom the auditory cup and acoustic ganglion had been removed, both on one side and on both sides, he concluded that in the tadpole the ear-vesicles are essential to the development of the power of equilibrium. He found that when both vesicles are removed no other organ compensates for their loss and that the animal is completely and permanently helpless as regards the maintenance of equilibrium; but that when one vesicle alone was taken out the remaining one was capable of performing the work of both so perfectly that the casual observer would mistake the tadpoles for normal individuals. Streeter further found that with transplantation of

ear-vesicles the group of cells forming the auditory cup are specialized to the extent that, although removed from the normal environment, they still contine to differentiate themselves into a structure approximately like the normal labyrinth. A nerve ganglion develops and complete nervous connection is established between the transplanted vesicle and the brain at an abnormal place. Later (*1506*) he found that a left vesicle transplanted to the right side developed into a perfect labyrinth in form and relations to the brain, but maintained its left-sided functional character. Schaefer (*1373*) demonstrated that invertebrates show no unusual phenomena after rotation and that such phenomena do arise in tadpoles after the complete development of the canals. Alexander (*30*) showed that ocular and other effects result from rotation in new-born children, the canals in such subjects being fairly well-developed. Scott (*1399*) concluded from the disturbances in the resting state and from the character of an animal's movements that the ear is essentially an equilibratory end-organ. Warren (*1610*) used a new method of observation during rotation and concluded "that the end-organ of the internal sense of rotation is in the head alone, since movements of the lower extremities are open to such absolute misjudgments." He further concluded that the ear was the portion of the head concerned and that it subserved a specific equilibratory function.

A few observers have sought to relate seasickness to affections of the semicircular canals and to identify the events occurring during seasickness with those taking place subsequent to artificial vestibular excitation. Enough evidence has been brought forward by Binz (*236*), Bonnet (*255*), Byrne (*380*), Hagen-Torn (*717*), Pincussohn (*1239*), Spira (*1446*), and Wojatschek (*1668*), to make the alleged relation plausible. The question has been raised again, more recently by Jones (*839*) and the conviction has gradually grown that the rolling movement of a vessel serves to stimulate the equilibratory organs.

4. *Experimental objections and exceptions.* Evidence contradictory to that already presented has been surprisingly authoritative and persistent; but such evidence must be treated critically for reasons that have been stated above (p. 14). It was assumed by many investigators that if it could be shown that sectioning the canals or causing other disturbances did not impair the equilibratory functions or, conversely, that if, under these conditions, compensatory movements still persist during vestibular stimulation, then the case was

strong against the ear as a special equilibratory organ. It is doubtful, however, whether this assumption can be made with any degree of assurance that it will hold. We have found, so far, that the evidence offered for the equilibratory functions of the canals has been *circumstantial* only. None of it has definitely shown that the canals are the *sole* organs of equilibration. In fact, there is a great deal of evidence to show that several end-organs may be involved in the appreciation of disturbances of equilibrium and in the arousal of compensatory movements. For example, Gruenberg (*702*) rotated about frogs a cylinder made up of alternate black and white strips. "Frogs placed in the middle of this circus arrangement could be made to turn their head and to give nystagmus or back-jerk by revolving the cylinder the same as when the animals themselves were rotated on the turn-table." Hadley (*716*) performed the same experiments with the lobster, and Fridenberg (*624*), Anderson (*52*), Knapp (*876*), Rádl (1273), Steiner (*1484*), Sternberg (*1495*), and Trowbridge (*1552*), have insisted that visual factors play a large part in maintaining balance. In stating the following facts, therefore, it must be remembered, first, that where the loss of the canals did not impair equilibratory functions, the investigations may not have been accurate enough to distinguish between the amount of adjustment possible in terms of other means of equilibration; and secondly, that where compensatory movements still arise when the canals are violated other end-organs may again be responsible.

Lussana (*1007*); Tomascewicz (*1538*), and Böttscher (*293*) found all the phenomena in response to rotation continued as in normal animals when the canals were removed or the auditory nerve cut.[17] Tomascewicz was able to remove the canals of fishes without finding the slightest trace of disturbances of equilibrative power. Kiesselbach (*864*) cut without result the horizontal canals on one and on both sides of carp. Sewall (*1406*) found no evidence in sharks and skates that the canals are the organs of equilibrium; but Lee (*958*, p. 192) criticizes his work because he studied only the immediate effects of the operations. Such a limited observation would prevent him from deducing any facts regarding more remote occurrences in

[17]Many investigators have called attention to the fact that cutting the canals or the auditory nerve did not interfere with the appearance of the events usually resulting from rotation. Such evidence, however, is not necessarily significant. Nystagmus may be induced without the canals. Furthermore, Delage and Purkinje are undoubtedly correct in assuming that some of the effects of rotation depend upon the inertia of the soft parts of the trunk and of its appendages. See below, p. 30.

the animals operated upon. Baginsky (*83*, pp. 444-445, *88*) cut the auditory nerve; but all phenomena continued the same as in normal animals, and Steiner (*1479*) found that many compensatory movements took place in frogs whose fore and mid-brains had been removed. In like manner Steiner (*1482*) found it possible to cut and to remove all six canals in Scyllium without causing any disturbances of movement. Removal of otoliths or attempts at removal invariably caused disturbances, usually a rolling movement to the operated side. But removing the entire contents of the labyrinthine cavity or filling it with paraffin did not affect locomotion! Other disturbances led this author to conclude "dass die halbzirkelförmigen Canäle der Haifische so wenig wie der N. acusticus zu den Bewegungen resp. deren Gleichgewicht in irgend welcher unmittelbaren Beziehung stehen und dass die Störungen welche man nach mechanischen Angriff auf den Vorhof thatsächlich beobachtet Zwangsbewegungen sind, welche, ihre Ursache in einer mittelbaren Läsion des Nachenmarkes an der centralen Ursprungsstelle des Hörnerven haben." A later report (*1483*) confirmed these results. Cyon (*459*, pp. 250 ff.) likewise found all phenomena in response to rotation continued as in the normal animal even after the removal of the canal and the cutting of the auditory nerve.[18]

Pursuing an attack through the ontogenetic and phylogenetic history of the ear, Ayres has followed an example set by Beard (*166*, *167*) and others and has drawn the conclusion that the canals are specially modified lateral line organs that have no relation whatever to equilibrium. Beard had stated that the two systems of organs were phylogenetically the same, the ear being nothing more or less than a modified portion of the system of the lateral line. Convinced that the disturbances described by other investigators were due to cerebellar lesions caused by too extensive an operation, the cerebellar peduncles being particularly affected, Ayres (*65*, *66*, p. 225) concluded that "the semicircular canals are in no way auditory or equilibrative in function." Clapp (*412*, *413*), Fuchs (*633*), Johnson (*830*), Moodie (*1124*, *1125*), and especially Parker (*1206*, *1207*, *1208*), have also studied the lateral line organs, but, for the most part, with contradictory results. Bunting (*358*) was unable to detect in large crayfish any inclination to rotatory locomotion when they were revolved on a horizontal turning table, and Strehl (*1513*) and Bech-

[18]See also Lucae (*998*), Preyer (*1250*), Schäfer (*1369*, *1373*), and Hensen (*752*).

terew (*174*) found all the phenomena in response to rotation continued as in normal animals when the canals were gone or the auditory nerve was cut. Bechterew (*173*, p. 516), in fact, concluded that the cerebro-spinal fluid served just as well as the fluid in the canals and that the gray matter of the third ventricle was the equilibratory organ.[19]

After having considered many of the objections raised at various times against the semicircular-canal theory, and especially on account of those investigations which seemed to show a difference when the eyes were opened or closed, Gruenberg (*702*) sought to find a reason for the discrepancy. First he noticed that during rotation to the right the head of a frog turned always to the left, no matter what the position of the frog; *e. g.*, rotation with head or tail first or with the right or left side first. That is, the animal was responding uniformly to what was, apparently, a change of stimulus. Lyon (*1012*) had already called attention to this fact, as had also Ewald (*562*), and Schäfer (*1369*). It was partially on this account that Cyon (*460*) had rejected the entire theory of the semicircular canals and substituted a theory of space-localization. After reviewing the conflicting evidence, Gruenberg found that two kinds of motion are present during rotation (provided rotation does not take place about an axis passing through the body of the animal rotated). He has shown that the vestibular responses are excited by a spin, which other observers may or may not have taken into consideration.

5. *Theoretical basis of other functions.* In spite of the growing body of evidence that an equilibratory receptor existed in the ear, it was not easy to break away from other apparent functions of the canals. The tridimensional distribution of the canals and their proximity to the auditory structures naturally suggested auditory functions. We have already seen that it was many years before the observations of Flourens could overcome the belief that all of the internal ear was auditory in function. Although Harless, Czermak, Brown Séquard and Vulpian (see *667*) confirmed the observations of Flourens, they, together with Böttscher (*292*), Lussana (*1007*), Läborde (*428*) and Tomascewicz (*1538*), insisted that the whole of the inner ear was really auditory in function. "Bis zum Jahre 1870 betrachtete man das gesamte häutige Labyrinth als Sitz des Ge-

[19]Elsewhere, however, Bechterew (*172*, p. 347) seems to have assigned more importance to the canals.

hörsinns."[20] After a short description of the canals, M'Kendrick and Gray concede that "these general anatomical facts support the supposition that the canals and ampullae are connected with the sense of hearing" (*1121*, p. 1194). They conclude their summary of the functions of the canals by leaving the question still open (p. *1205*). M'Kendrick suggests that in the absence of definite proof of the equilibratory functions of the canals, they may be concerned in hearing if the wave motion is considered as creating pressure at the mouths of all the canals at once, thus causing the supposedly elastic membranous canals to expand slightly and furnishing a stimulus to end-organs similar to that found in the cochlea. Still more recently Wrightson (*1677*, *1678*, *1679*) has emphasized a theory of audition first proposed by him in 1876 in which the whole of the inner ear is alleged to be affected by mass movements of the lymph. A similar conception has been urged by Bayliss (*164*), Deetjen (*491a*) and Frey (*613*).

Most of the writers urging other than equilibratory functions for the canals have stumbled over the structural similarity and proximity of the canals and cochlea and over the fact that the canals have such a curious tridimensional arrangement. One is inclined to believe that a teleological bias may be at the basis of some of the functions that have been attributed to an apparatus which invites in a unique manner just such speculations.

The leading exponent of the doctrine that the canals mediate the perception of the direction of sound was Cyon.[21] (See Crum Brown, *442*). Cyon's theory was strengthened by the facts noted above which seemed to throw doubt on the prevailing notion of vestibular functions. The characteristic position of the canals in the three planes suggested immediately, of course, tridimensional space. We have already seen that quite early Autenrieth (*64*) had proposed the ear as an organ for the appreciation of the direction of sound. In this proposal he was seconded by Ogston (*1185*) and by Block (*245*), whose thesis appeared just before Cyon began his long series of articles on the subject (*453-479*). Cyon's first statement of

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[20]Nagel (*1166*, p. 790).

[21]The suggestion has even been made that the canals are organs for the appreciation of noise. See Nagel (*1166*) and Fridenberg (*617*) for references. Considerable work was done in order to determine whether an animal without semicircular canals could still perceive sounds. Here again, however, the evidence is contradictory as reference to Ewald (*665*), Wundt (*1681*, *1682*), Kuttner (*927*), Matte (*1085*), Bernstein (*211*), and Strehl (*1513*) will show.

his theory appeared in 1874 (*478*, p. 38). It was followed in 1876 (*454*) by a study of the relations between the ears and the eyes that gave him a clue to all of his further work. The theory aroused a storm of discussion, important facts being contributed by Bonnier (*270*, *271*), Chauveau (*405*), Couturat (*434*), Croom-Robertson (*437*), Doniselli (*529*), Duvall (*541*), Fridenberg (*619*, *620*, *622*), Golla (*666*), Gueroult (*705*), Lipps (*985*), Preyer (*1250*), Reinhold and Alt (*1293*), Wlassak (*1659*), Woerkom (*1663*) and many others.

Cyon holds that knowledge of the position of bodies in space depends upon nervous impulses coming from the contracting ocular muscles; that the oculo-motor centers are in intricate physiological relations with the centers receiving impulses from the nerves of the semicircular canals; and that the oculomotor centers, thus excited, produce movements of the eyeballs, which then determine our notions of spatial relations. Cyon's point of view can best be gotten from his own words. To quote: "Les canaux semi-circulaires sont les organes périphériques du sens de l'espace; c'est-à-dire que les sensations provoquées par l'excitation des terminaisons nerveuses dans les ampoules de ces canaux servent à former nos notions sur les trois dimensions de l'espace. Les sensations de chaque canaux correspondent à une de ces dimensions.

"À l'aide de ces sensations, il peut se former dans notre cerveau la reprèsentation d'un espace idéal sur lequel seront rapportées toutes les perceptions de nos autres sense qui concernent la disposition des objets qui nous entourent et la position de notre corps parmi ces objets."[22]

"La disposition des nerfs, dans trois plans perpendiculaire l'un à l'autre, se prête à merveille pour une pareille fonction. Nous pouvons très bien nous figurer comment les sensations d'étendue, dans trois plans, dont la disposition, chez tous les vertébrés, repondent exactement aux trois co-ordonnées de l'espace, peuvent être utilisées par notre intelligence pour la construction d'une notion de l'espace.

"Je dirais plus: aucun autre sense ne présente une relation aussi facile à saisir entre la représentation et la sensation, que le sens d'espace, d'après ma manière de voir."[23]

The canals are thus the peripheral organs of the sense of space,

[22] See Cyon (*457*, p. 64).
[23] *Ibid.*, p. 73.

and the sensations caused by excitation of the nervous terminations in the ampullae assist in forming our notions of the three dimensions, the sensations excited by each canal corresponding to one dimension. Cyon was undoubtedly led in this direction because of a further compromising of the static and dynamic functions, theoretically assumed, of the canals through experiments performed by himself. Quite early (*457*) he had punctured the canals and drawn off the endolymph, replacing it with gelatine. Then putting pieces of laminaria into the canals, he produced great changes in pressure and found that no disturbances of equilibrium resulted. All of Cyon's earlier work proceeded upon this empirical level but later work has become involved with larger philosophical speculations (*475-479*).[24] One cannot be sure that one's analysis of Cyon's position is correct for he frequently uses offensive personal remarks against those not agreeing with him and his theory has not received, therefore, the full consideration it may deserve. Nagel (*1166*, p. 804) describes the situation thus: "Die Art, wie v. Cyon sich das Bogengängsystem als Quelle der Raumvorstellung tätig denkt, ist mir, wie ich offen gestehen muss, nicht verständlich geworden, weshalb ich auf näheres Eingehen auf seine Theorie (wenn von einer solchen zu reden ist) verzichten muss."

Very similar to Cyon's position and yet also including a strictly auditory function is that of Preyer (*1250*).[25] He "versuchte die Gehörsfunktionen der Bogengänge zu retten durch die Annahme, dass die specifische Energie der Ampullen-nerven sei, ein mit Schallverbindenes Raumgefühl zu geben, und zwar ein Richtungsgefühl." Objections to such theories are obvious. The inaccuracy of our ability to localize sound does not suggest the presence of a special organ; although Münsterberg (*1149*) and McBride (*1098*) have suggested the aid in localization given by reflex movements of the head excited in the ear. The evidence is quite conclusive, however, that the appreciation of the direction of sound does depend upon certain other and well-defined conditions. Crum Brown gives two

[24] "Meine alteren Untersuchungen haben ergeben, dass der Bogengangapparat als das geometrische Sinnesorgan betrachtet werden muss. Wir haben eben gesehen, dass das Corti'sche Organ das Recht beanspruchen kann, das Organ des arithmetischen Sinnes zu sein; mit einem Worte, das Ohrlabyrinth enthält zwei mathematische Sinnesorgane für Raum, Zahl und Zeit. Die Richtung ist ihrem Wesen nach untheilbar und unbegrenzt. Wir verdanken also unsere Vorstellungen ebenfalls der Unendlichkeit des Raumes und der Zeit von den Richtungsempfindungen der Bogengänge." See Cyon, (*477*, p. 533.)

[25] See also Frey (*613*), Kries (*911*), and Nuvoli (*1182*).

convincing arguments against the theory. The canals cannot be the organs for perceiving the direction of sound for (1) the shortest possible wave we can hear is so long compared with the dimension of the ear that every part of it must be in some phase of the wave and (2) experiments show conclusively how we do perceive the di-direction of sound (*446*). Külpe (*924*, p. 150) finds that "despite its apparent support by the spatial arrangement of the three canals the hypothesis is exceedingly improbable, for the reason that there is absolutely no proof of a uniformity of relation between the spatial positions of the sound-producing body and the various points of excitation of the vestibular nerve."[26]

6. *Summary and conclusion.* We have found that the similarity of the responses excited by whirling, those excited by violating the integrity of the cerebellum, and those excited by disturbing certain portions of the inner ear, has been successfully demonstrated. We have also found that the presumption of a new receptor in the inner ear was put to a thorough laboratory test and that while the evidence has been contradictory, the opinion has been constantly growing in weight that the inner ear does contain a specific kind of receptor and that this receptor is primarily concerned in the mediation of disturbances of bodily equilibrium. It has been shown to be probable that this receptor lies in the semicircular canals. Not enough evidence has been submitted to show that this part of the ear is involved in any way in the mediation of auditory qualities or in the perception of the direction of such qualities.

It is necessary, however, to distinguish with care between the conclusion that the canals in the ear are very closely related to disturbances of equilibrium and the supposition that the canals are the sole organ responsible for the appreciation of a disturbed balance. All of the evidence that has been offered is circumstantial only. It is true that whenever the canals are to any extent disturbed defects of equilibrium appear. It has not been made clear, however, that the perception of rotation or other similar events is mediated *solely*

[26]For other papers dealing with the questions so far discussed see Adler (*5*, *6*), Alexander (*10-32*), Chevreul (*407*), Curschmann (*450*), Czermak (*480-482*), Dalby (*484*), Dentz (*515a*), Denker (*514*, *515*), Delage (*499-510*), Echert (*546*), Engelman (*553*, *554*), Ewald (*557-571*), Gad (*634*, *635*), Gelle (*647*, *648*), Girard (*655*, *656*, *657*), Garrault (*642*), Gottwald (*670*), Güttich (*710-713*), Hartmann (*727*, *728*), Henri (*747*, *748*), Hesse (*764*), Ilyin (*813-816*), Jensen (*826*, *827*), König (*890-892*), Laborde (*928*), Lange (*942*), Laudenbach (*947-951*), Leydig (*983*), Michalski (*1114*), Morison (*1131*), Munk (*1147*, *1148*), Onimus (*1189*), Ogston (*1185*), Retjo (*1296-1299*), Strehl (*1513-1515*) and Verworn (*1585*, *1586*).

or even directly by the ear because the responses to rotation happen to be the same as those resulting from mechanical injury to the ear or to the cerebellum or to the VIIIth nerve. We can only conclude, therefore, that the internal ear is the seat of a receptor which stands in very close functional relationship with the equilibrium of the body. The evidence that has been offered can warrant no more positive conclusion.

B. *The Anatomy of the Receptor: Its Significance.*

The descriptive anatomy of the canals and of their seat with reference to the head was written early, and the question has never since aroused much argumentative discussion. The refinements made possible by keener anatomical instruments and more adequate phraseology have not changed in any essential aspect, therefore, such descriptions of these organs as were originally given by Crum Brown (*439*, *440*), Ewald (*562*), and Hasse (*730*, *731*, *732*), the latter being, apparently, the pioneer in the field with minute descriptions of the canals of birds, frogs and fishes.

1. *General anatomy.* Although we are not here concerned with the details of the minute anatomy of these organs, there are several general facts of anatomy and of research that are of interest. (a) In the first place, the position of the canals in the head gives them a prominence equal to that of other end-organs in the head-segment, in so far as their relations to the rest of the body are concerned. The cephalic end of the body has generally been described as the exploratory end; if, then, the canals are equilibratory in function, their location in the cephalic segment would serve admirably to furnish, through the head, information to the whole body concerning the position of the organism in space. (b) In the second place, the structure of the canals themselves is significant. They lie in three planes, as we have already noted. The circular form of the canals would suggest that they might in some way control a variety of movements of the head in any plane.[27] As they are arranged it becomes manifestly impossible for exploratory movements of the head end or for movements of the body as a whole to occur without bringing into play the receptor organs of the head. (c) And, finally, there is a good deal of evidence to show that the struc-

[27] See Weiland (*1618*), and Yearsley (*1684*). The paper by Yearsley is for the most part a translation from Delage (*506*).

ture and stage of development of the canals and of their corresponding central connections parallel the ability of the organism to maintain balance. For example, Rawitz (*1282-1286*), Cyon (*468*) and Alexander and Kreidl (*37-40*) believed they had discovered structural peculiarities which would explain the unusual behavior of the dancing mouse. But Kishi (*868*), Panse (*1195*, *1196*, *1197*) and Wittmaack (*1655*) contradicted this evidence.[28] After summarizing these and other articles, Yerkes (*1687*, *1688*) concluded that the ear was probably unusual in form but, in view of the lack of conclusive evidence, he was inclined to explain the peculiar behavior of the dancing mouse in terms of the structure of the whole organism. Gray (*686-692*; especially *688*) is inclined to believe that the form and structure of the canals are of considerable significance so far as the ability of the organism to make movements is concerned. His point of view may be seen in such statements as this: "Thus the sloth, apparently as a result of its sluggish movements and circumscribed area of habitation shows a diminution both in the size and delicacy of outline of its canals, while the cochlea is as well developed as in other animals." Still further evidence has been sought by correlating equilibratory ability with the genetic development of the canals. Alexander (*30*), for example, has studied new-born children, and Winkler (*1646*) new-born rats. We have already referred to Streeter's (*1505*) treatment of tadpoles. Prince (*1252*) found that in kittens vestibular reactions progress *pari passu* with the development of the equilibratory mechanism.

2. *Specific anatomy.* This is not the place to give a detailed account of the minute anatomy of the semicircular canals but it can be said that this problem has deserved and has had the best minds and the best instruments directed toward its solution.[29] The monumental work of Retzius (*1301*) and of Gray (*688*) illuminated by Alexander's observations (*12*, *14*, *15*, *18*, *20-23*) on the pathological anatomy of the canals has left little to be desired. Of the early descriptions of the canals, those of Crum Brown (*442*) and of Ewald (*562*, *571a*) are the most satisfactory. Crum Brown's method of measuring the parts of the ear (*1120*) was adopted for many years, while the accuracy of Ewald's work was such as to excite the en-

[28] See also Lennep (*969*), Quix (*1266*), Röthig (*1333*), and Zoth (*1699*, *1700*).

[29] Some interesting models and reconstructions have been made of the equilibratory apparatus. See Bezold (*224*), Ewald (*571a*), Downey (*531*), Goldstein (*662*), Girard (*657*), and Rauch (*1281*).

thusiastic admiration of such a critic as Nagel (*1166*, p. 779). Breuer (*316*), as we shall find, was one of the most far-sighted of the early workers upon the canals and his anatomical observations and comments were no small contribution in the early stages of the problem. The additions and emendations that have brought knowledge of vestibular anatomy to its present level can be easily discovered in the work of Bechterew (*176*), Brünings (*346*), Cole (*423*), Delage (*506*), Fraser and Dickie (*611*), Girard (*657*), Goldstein (*663*, 664), Gordinier (*669*), Hartmann (*728*), Hopkins(*784*), Ibsen (*808-810*), Mada (*812*), Kaiser (*846*), Katz (*855*), Kolmer (*889*), Koppen (*893*), Kuhn (*920-923*), Leidler (*969*), Matte (*1084*), Meyer (*1113*), Muskens (*1157*), Porta (*1246*), Randall (*1277*), Reeder (*1287*), Reich (*1289*), Schilling (*1380*), Schoenemann (*1389*), Sgobbo (*1409*), Shambaugh (*1413*), Siebemann (*1428*), Sonntag (*1435*), Steinbrügge (*1478*), Stenger (*1487*), Streeter (*1512*), Thomas (*1530*), Trendelenberg (*1543*), Trendelenberg and Kuhn (*1546*), Treviranus (*1547*), Troltsch (*1550*), Vincenzi (*1593*), Voit (*1594*), Weiland (*1618*), Wenig (*1623*), Westphal (*1624*), Wittmaack and Laurovitsch (*1656*), Wollenberg (*1672*, *1673*), Wulf (*1680*) and Yearsley (*1684*). Of late a great deal of interest has centered about the structure and location of the equilibratory end-organs themselves; that is to say, about the hair-like endings on the ampullar structures and about the otolithic structures in the utricle and saccule. No little information has been gleaned from studies on comparative anatomy. Of the studies upon this problem those by Deiters (*497*), Denker, (*514*), Gille (*647*), Gunther (*708*), Hyrtle (*807*), Kollmer (*887*, *888*), Köppen (*893*), Leydig (*983*), Magnus (*1074*), Panse (*1194*), Rathonyi Reusz (*1279*), Rothig and Brugsch (*1334*), Rüdinger (*1339*), Schrader (*1391*, 1392) and Sato (*1365*, *1366*) have been the best.

3. *Summary and conclusion.* It is apparent, therefore, that the vestibular portions of the inner ear are so placed and so constructed as to make it entirely possible for equilibratory functions to be ascribed to them. We are not justified in making teleological comments, however, as has been the tendency of a good many writers.[30] Moreover, the analogy between the position of this end-organ and that of the other end-organs in the head cannot be carried

[30]For example, "everyone must see that an apparatus so purpose-like in its arrangement must have a use, and this use must be one applicable to all the higher animals. . . . The apparatus is admirably fitted to act as the organ of the sense of rotation." Crum Brown (*444*, p. 451). See also Fridenberg (*618*), Brückner (*336*), and Hensen (*751*).

too far. It is probably true that the eye is the sole organ for the mediation of visual qualities although, on occasion, the surface of the skin may be grossly sensitive to light. The same is true of the cochlear portion of the ear. It cannot be said, however, that this must also be true of the canals. In other words, we return once more to the conclusion that although the ear is closely related to the functions of equilibration, it may not be the sole organ of balance.

C. *The Mode of Excitation of the Receptor: the Principle of Inertia.*

In striking contrast to the great amount of experimental work done in isolating the receptor is the relatively small amount concerned with its mode of excitation. In describing the mode of excitation of the other end-organs, it is fruitful to point out the principle of explanation upon which the facts may be explained. In vision, for example, the principle commonly appealed to is that of reversible chemical processes. In audition, frequent use has been made of the principle of sympathetic resonance. In a similar way, investigators interested in the semicircular canals have appealed to the physical principle of inertia. This principle has been used in at least three different ways. We shall consider them in order.

1. *The inertia of the soft contents of the body.* In the first form, represented by Purkinje (*1257*, p. 79), an explanation of the facts of rotation was sought by supposing that "during the rotation of the body about its longitudinal axis, the brain, in virtue of its soft consistence, ought to have a tendency to remain a little behind the movement of the skull."[31] Purkinje stated that this was the "same phemomenon which we observe in a liquid when the vessel containing it is set in rotation. The particles of the liquid preserve their position relative to the external space, until their adhesion to the walls of the vessel forces them to take part in the motion of the latter. The cohesion of the brain is too great to allow of the reproduction of the same phenomena; but as the brain is soft and capable, to a certain extent, of internal displacement, it has some of the properties of liquids. We must admit that a movement more or less intense must produce a displacement and relaxation of parts although an actual rupture of continuity cannot occur. Such distortions should

[31]See also Aubert (*62, passim*), M'Kendrick and Gray (*1121*, pp. 1196-1197), and Nagel (*1166*, pp. 762-770).

produce the same disturbances as actual mechanical lesions, and differ from them only in degree." Crum Brown, who later became one of the most extreme advocates of the principle of inertia in the ear, agreed in his earlier experiments that Purkinje's explanation might be partly true in describing the facts of rotation where the turning is very rapid and is suddenly stopped (*442*, p. 634). He also suggested that because there is an adequate stimulus for all the other sense-departments, in any one of which excessive amount of the same adequate stimulus will produce wide-spread irritation, just so "it is not unreasonable to suppose that sudden and violent changes of rate of rotation should be perceived by the shock communicated to all the soft and movable parts of the body, although slighter changes may be perceptible only by the special organ of the sense of rotation." (*442*, p. 658). Ten years later, Aubert explained dizziness as sensations stimulated by inertia and centrifugal moment in the cerebellar mass or its delicate coatings (*62*). More recently Cattell (*401*, p. 100) has stated that the evidence for the part played by the canals is circumstantial and inconclusive, that equilibrium and knowledge of motion are probably the outcome of a very large number of conditions. He urged that the vestibular lymph played a part, but that the inertia of the soft parts of the head was important. Rotation causes congestion in the cortex and viscera. To quote: "It would seem that our instinctive knowledge of equilibrium and of a motion of the body as a whole depends on very complex sensory impressions. One of these is very probably the pressure due to inertia of the perilymph and endolymph of the semicircular canals; but it is quite possible that the inertia of the head and body are more important factors. Rotation of the body would tend to cause congestion of the brain cortex by centrifugal action, and the resulting dizziness would be analogous to that accompanying intoxication or fever. The position of the body as a whole affects not only the circulation of the blood, but also the pressure of brain, viscera, etc., and the alterations in the direction in which gravity acts would cause important changes in muscular tensions. Motion of the body as a whole would cause pressure of the soft parts of the body on those more hard and skin sensations (due to inertia of the body as a whole) would occur at points where the body touches other things."

In 1909, Holt (*783*) emphasized the inertia of the trunk, limbs, and internal organs, and even of the blood as contributing to the perception of motion. He also quotes Delage as mentioning sensations

"produced by a sort of internal tidal movement in which all the liquids and such solid organs as have any mobility participate."[32] Schäfer (*1369*), Breuer (*313*), Mach (*1015*), and Abels (*1*) also felt that at least some of the processes concerned in the perception of motion came from the same sources, even though Mach has elsewhere said that "one can scarcely explain feelings of motion in terms of skin or muscle sensations, in view of the feelings in the head, the enormous influence of the head position and the Flourens' experiments." M'Kendrick and Gray mention the experiment of Cyon in which a rabbit was rotated after the auditory nerves had been cut and found that the responses were the same as in normal animals. "This observation would at first sight appear seriously to compromise the statical and dynamical theories; but what it really does is to show that some of the phenomena of Purkinje may, as he himself supposed, be due to the action of rotation on the brain itself. If so, one would expect to see these phenomena after the division of the auditory nerves, and the fact does not invalidate the reasoning on theoretical and experimental data regarding the functions of the canals already described. (*1368a*, p. 1202).

2. *The inertia of the limbs and of the head.* The application of the principle of inertia to the appendages of the trunk is of the same general kind as found above. The classical example of this use is found in Schäfer, who succeeded in demonstrating to his own satisfaction that the responses to rotation were due solely to the inertia of the loosely-jointed head (*1369*). He accomplished this by means of a wooden model which behaved on the turn-table just as a frog or pigeon does. Account has also been taken at various times of the inertia of the whole body and of the arms and legs (*783*).

3. *The inertia of the liquid in the semicircular canals.* In the hands of Mach, Breuer, and Crum Brown,[33] the principle of inertia took on a new significance. Goltz, (*667*) in opposition to Lussana (*1007*) and Curshman (*450*) assumed, as did also Moon (*1126*) and

[32]The reference to Delage is as follows: "Die Empfindungen der Fortbewegungen sind wahrscheinlich allgemein, hervorgebracht durch einen Druck der Flussigkeiten des Organismus gegen die Gefäge und die Wandungen ihrer Behälter, durch einen Jug der verschiedenen Eingeweide an ihren Anheftungstellen und an ihren eigenen Teilen, und vielleicht durch eine Worte, durch eine Art von Ebbe- und Flutbewegung aller Teile unseres Organismus, welche eigene Beweglichkeit haben." Cf. Nagel (*1166*, pp. 802-803). See also Delage (*506*), and a translation of this paper by Yearsley (*1684*).

[33]The conclusions of these men were attained independently and first published within six weeks of each other. Nagel (*1166*, p. 801) called the promulgation of the

Stefani (*1450-1452*), that the canals were organs which, by differences of pressure in different parts of the system, gave a perception of the position of the head in space. "Wir wollen annehmen, daz die in den Ampullen vorhandenen Nervenendigungen in ähnlicher Weise geeignet sind, durch, Druck oder Dehnung erregt zu werden. sie etwa die dem Drucksinne dienen enden Nerven der äuzeren Haut. Die in den Bogengängen befindliche Flussigkeit (Endolymphe) wird nach bekannten physikalischen Gesetzen diejenigen Abschnitte der Wandung am starksten ausspannen, welche am meisten nach abwärts gelegen sind. Je nach der Stellung des Kopfes wird die Verteilung des Druckes der Flussigkeit wechseln, und einer jeden Kopfhaltung wird demgemäss immer eine bestimmte Form der Nerven erregung entsprechen" (*667*, p. 187 ff.). The modified view regarded them as organs, which, by virtue of the contained liquid and moveable soft parts mediated a perception of the change of positior of the head. Mach, first stating his theory in 1873 (*653*, *654*) departed the least from Goltz's static view. He supposed that with every change in the position of the head there occured a change in the pressure of certain parts of the canals, thus furnishing the conditions for the excitation of the end-organs in the canals. It was hard to understand, however, how a change of pressure could occur without the introduction of some flowing movement in the liquid. The change in the theory here stressed was no doubt the source for the later belief that only changes in the speed of movement were perceived. In swinging from a static to a dynamic view, Mach, Breuer and Crum Brown neglected all the value that the static view has. As a matter of fact, the belief that we sense only changes of acceleration has become common among scientific men as well as among the laiety. It is evident from recent analyses of the apprehension of rotation, however, (see Griffith, *697*, *698*) that there is a continued excitation of large groups of muscles during the whole time that rotation continues unchanged in acceleration. The writer believes that the distinction between the perception of

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theory a brilliant mental achievement. He further says: "Die Mach-Breuer-Brownsche Theorie der Labyrinthfunktion in ihrer durch Breuer hinsichtlich der Otolithen-apparate ergänzten Form steht meines Erachtens in ihren wesentlichen Grundlagen heutzutage unbestreitbar festgegründet." Holt (*783*, p. 382) believes that in the main the theory is established beyond all question. Nagel (*op. cit.*, pp. 790–801) gives an excellent summary of the theories and is inclined to give Mach and Breuer the honor of originating them, not, however, detracting from the achievements of Crum Brown (p. 790, note). See also for a summary, Peters (*1217*, pp. 47-76).

motion and of the change of motion rests upon the assumption that the complexity of mental processes resulting from the starting and stopping periods has secured attention to the exclusion of the processes which actually continue through the whole period of vestibular excitation. There is a perception, then, both of movement and of changes in acceleration. The fact that we do not perceive the direction or the rate of movement of the body through space in company with the earth is not an analogous case. In the first place, the medium in which we live is moving with us, a fact that does not hold for rotation in a chair. In the second place, if the race ever did perceive the rotation of the earth or of its almost linear movement about the sun, it has been shown that a few days practice will serve to eliminate all such perception save as it is given by extraneous factors dependent upon an environment that is not rotating at the same time. Finally, Gruenberg has shown that the adequate stimulus for exciting the canals is an alleged 'spin.' Certainly, this 'spin' effect is below any limen of sensitivity so far as the earth and the human organism are concerned. Working on this basis, Breuer[34] modified the theory to the extent of supposing that there were currents in the liquid in a direction opposite to that in which the head was moved. Hitzig (*771*) was the severest early critic of the Mach-Breuer theory and more recently Cyon (*478*, p. 49) has also dealt with it severely.[35] Cyon's experiments of introducing into the canals dry pieces of laminaria which gradually swell by absorbing moisture and thus increase the pressure did much to discredit Mach's view. It seems, however, that such violent disturbance must have vitiated observations to some extent at least. Cyon also observed that periodic changes of pressure occur in the contents of the labyrinth synchronous with the heart's beat; but Crum Brown insists that this pressure must occur synchronously in all the ampullae and hence the resultant rotation perceived would be zero.[36] When the head stops the liquid will move on slightly. Under these two movements, the hair-like endings of the nerves are excited and appropriate sensory processes set up. Mach's interpretation soon became an objection to Breuer's dynamic theory. Mach held that

[34] Breuer's hydrodynamic theory was first stated in 1873. See Breuer (*311*, *312*, *314*, *315*, *316*, *317*).

[35] Bárány and Wittmack (*144*, pp. 39-46) have also critically discussed the theory.

[36] See Crum Brown, (*442*, p. 657).

the small bore of the canals would preclude all movement because of friction; hence his appeal to change of pressure only.

Crum Brown went still further and insisted that the whole liquid and membranous contents of the bony canals lag behind.[37] He further insisted that all six canals were essentially one organ, the canals being arranged in pairs and functionally complementary for each plane of space, so that movement of the head in any direction was appreciated. ". . . the six canals are sensibly parallel two and two. Thus the two horizontal canals are in the same plane, while the superior canal of one side is in a plane nearly parallel to that of the posterior canal of the other side. Further, in each of these three pairs the two canals are so placed that when rotation takes place about the axis to which they are perpendicular, one of the two canals moves with its ampulla preceding the canal, so that flow from ampulla to canal alone stimulates the hair-cells, while no effect is produced by flow in the opposite direction, we have in the six canals a mechanical system capable of giving us an accurate notion of the axis about which rotation of the head takes place, and of the sense of the rotation." (*442*, p. 635)[38] In a much more recent discussion of the kinetic theory, Scott (*1399*) concludes that the theory is in no way vitiated by difficulties in the conception of currents through such small canals, for all that is required is the presence of positive and negative pressures in successive portions of the endolymph.[39] This need not require a flow of liquid at all. Scott's contention apparently finds a parallel in the propogation of sound waves. Mulder (*1143*) discovered that a subject felt at rest when rapid startings and stoppings followed one another and explained this fact by the consequent alternation of push and pull in the liquid of the canals. Maxwell (*1091*, p. 351), however, after changing by surgical means the plane of the horizontal canal in dog-fish concluded that "no further consideration need be given to the possibility of currents in the semicircular canals as the cause of the excitation which on rotation gives rise to the reflex compensatory movements. . ." He has found, nevertheless, that movements do take place in the ampullae and suggests that the canals act only as a means of equalizing

[37] Crum Brown first stated his thesis in 1874. See Crum Brown (*441*). This paper was elaborated in the same year (*439*). (See also 442-447).

[38] See also Goebel (*658*).

[39] See also (617, pp. 173-177).

the pressure. Rossi (*1328*) and Hoyt[40] have seen, by means of small models of the canals, the actual disturbances that take place during rotation.

4. *Summary and conclusion.*— It is clear, therefore, that the physical principle of inertia may be used to good advantage in a theory of the mode of excitation of the vestibular receptor. On the contrary, a naive application of the principle as it is found in physics does not fit all the facts. Furthermore, no evidence has been offered to show that the inertia of the soft parts of the trunk or of its appendages does not play a more or less important part in the perception of changes of position. On the other hand, there is some evidence to show that changes of pressure may occur in various parts of the canal-system and that this pressure affects the delicate hair-like organs in the ampullae giving rise to excitations that play an undetermined part in maintaining equilibrium. We are warranted, accordingly, in adding to our store of knowledge to the effect that the canals may play a relatively large part in the perception of rotation. We are not yet justified in assuming, however, that equilibration is mediated solely by this apparatus.

D. *Theories Regarding the Function of the Receptor.*

Once the existence of an equilibratory end-organ had been confirmed and a theory of its mechanism proposed, the next logical step was a more analytical statement of the functions attributable to the organ. The same kind of evidence adduced in favor of the former conceptions suggests also the functional differences here to be considered. The conclusion of Jones (*839*, p. 83) that the inner ear consists of "the acoustic labyrinth concerned exclusively with the function of hearing, the static labyrinth for the maintenance of station, and the kinetic labyrinth, for the recognition and analysis of motion" has its roots in some of the earliest statements made concerning the canals. At one time or another, at least four distinct functions have been urged for the vestibular portion of the internal ear.

1. *Static: the maintenance of bodily position.* The static and dynamic functions seem to have been the first proposed. On the one hand, it was believed that the internal ear must contain an organ for the appreciation of the vertical. For example, it has been

[40] See Maxwell (*1091*, p. 353).

pointed out by several investigators that, in lower forms, the otocysts may act as a 'geotropic sense-organ'.[41] On the other hand, the ear was supposed to contain an organ for the appreciation of actual movements of the body either of rotational or of translational motion. In translational motion the body is constantly orientated; while rotational movement about a bodily axis involves a change of orientation. In the case of the appreciation of the position of the body with reference to the vertical or to gravity, we have seen that the principle contribution of Goltz (*667*, p. 187) was his insistance that the canals were organs primarily designed for the maintenance of position, a statement indirectly confirmed by many subsequent observations that the head position is essential to orientation.[42] Cyon (*453*) developed with a good deal of detail the notion of Goltz that the equilibrium of the head was an important consideration.[43]

Although most of the literature relating to the static functions is closely associated with the other alleged functions of the canals and particularly with the supposed tonic control exercised by the canals, nevertheless, a fairly large number of titles deal specifically with the problem as formulated by Goltz. Becher (*169*), Buddenbrock (*335*), Bunting (*358*), Engelmann (*553*, *554*), Gad (*634*), König (*892*), Koranyi (*895*), Kramer and Moskiewicz (*897*), Laudenbach (*949*, *951*), Lyon (*1011*), Mangold (*1049*), Marcan (*1059*), Murbach (*1153*), Ruysch (*1357-1359*), Schäfer (*1370*), Stern (*1493*), Stimpson (*1500*), Thomas (*1531*), Urbantschitsch (*1573*), Verworn (*1585*), Weill (*1621*), and Wlassack (*1658-1659*) are a few who have considered, seriously, the "static sense."

2. *Dynamic: sensitivity to translational and rotational changes of movement.* We have already seen how Mach, Breuer and Crum Brown made the equilibratory receptor a dynamic mechanism. As a matter of fact, the dynamic functions of the canals are most commonly thought of whenever these structures are mentioned. But the distinction between the parts played by the semicircular canals, on the one hand, and the utriculus and sacculus, on the other, in mediating translational movements as opposed to rotational movements was not carefully drawn until Crum Brown came to the conclusion that the two kinds of movements were mediated by different end-organs. Following a suggestion given by Mach, Crum Brown

[41] See, *e. g.*, Loeb (*988*, *989*, *991*) and Wheeler (*1626*).
[42] See also Nagel (*1165*, *1176*, pp. 801-802).
[43] See, however, Wegener, (*1617*).

(*444*) proposed that the macula of the utricle was the end-organ for the mediation of movements in a straight direction. He supposed that this organ was set into function by the inertia of the contained liquid, as in the case of the canals. Warren (*1610*), on the other hand, concluded that "the organ for the sense of rotation is the same as that for progressive movement, even though this is contrary to Delage who denies that the sense-organ for progressive movements is in the head at all, although admitting it for rotary movement." Maxwell (*1092*, *1093*, *1094*) found no evidence that the functions of the otoliths and of the semicircular canals widely differ. In fact he has concluded that the otolith organ in the recessus utricli mediates most, if not all, of the static and dynamic functions ascribed to the ear. Clark (*414*, *415*), however, assigns them both to the canals. The evidence is, therefore, conflicting and inconclusive. Between these affirmations and the denials, however, lies a vast literature which cannot be ignored. In one manner or another the problem has been discussed and experimented upon by Belnior (*194-196*), Block (*245*), Brock (*327*), Carazzi (*394*), Chevreul (*407*), Dalby (*484*), Echert (*546*), Gellé (*648*), Gertz (*652*), Girard (*655*), Goldstein (*662*), Gottwald (*670*), Gradenago (*673-675*), Gradle (*676*), Grelle (*693*), Güttich (*710*), Heyde (*765*), Ibsen (*808*, *810*), Johannson (*828*), Laborde (*928*), Lafete-Dupont (*934*), Laudenbach (*947*), Lewis (*976*), Lugaro (*1005*), Lussana (*1009*), Malium (*1048*), Marikowsky (*1063*, *1065-1067*), Masuri (*1076*), Matte (*1082*, *1083*, *1085*), Michalski (*1114*), Moon (*1126*), Morison (*1131*), Muncy (*1146*), Ogston (*1185*), Passow (*1210*), Roncagli (*1321*), Schäfer (*1373*), Schiff (*1377*), Schilling (*1381-1383*), Shambaugh (*1415*, *1417-1418*), Spamer (*1442-1444*), Spear (*1445*), Stefani (*1451-1453*), Stein (*1457*), Steiner (*1481*), Stenger (*1485*), Stern, Bonnier and Kreidl (*1494*), Strehl (*1513*, *1515*), Swan (*1520*), Tsion (*1555*), Tullio (*1557-1560*), and Viguier (*1589*).

3. *Tonic.* The most interesting function ascribed to the canals is the tonic control which they may exercise over the whole bodily musculature. It will be recalled that Löwenberg (*995*) gave in 1873 an early hint of such a function. Although the most significant defense of this view comes from Ewald, a great number of investigators have made it a subject of special inquiry. So far no serious contradiction has been offered to the main points of Ewald's theory although the details have been generously modified now in one direction and now in another. Alexander (*29*, p. 76) says of it:

"In der Darstellung des Labyrinths als ein der Tonus erhaltendes oder den Tonus regulierendes Organ, steht die Ewald'sche Theorie unbestritten da."

Ewald suggested that all of the muscles of the body were kept in a state of tension or tone by means of the excitation from the labyrinth. He does not deny, however, that sound waves stimulate the nerve-endings also, and he suggests that in this way rhythmic movements of the muscles, as in dancing to music, may be facilitated. Meumann (*1111*) and Vaschide and Vurpas (*1581*) have defended the same view. Bechterew (*172*, p. 347) has also suggested the possibility. "Die semicirculären Canäle sind Organe, die nicht nur der Gleichgewichtserhaltung des Kopfes, sondern der des ganzen Körpers dienen. Zugleich stehen sie in sehr nahe functioneller Beziehung zu der Function des Gehörorgans. Die Einwirkung von Schalleindrücken auf die Bewegungen und den Gleichgewichtszustand des Körpers geschieht aller Wahrscheinlichkeit nach vermittelst der semicirculären Canäle."[44] Ewald suggested, furthermore, that injury to the canals must first affect those muscles whose movements were most delicate, such as those of the eye (as in nystagmus), while the grosser muscles are affected later in larger acts of compensation. After plugging the canals he found abnormal flaccidity. Ewald (*568*, p. 541) concludes: "Aus diesen zwölf Versuchen. . . darf ich den Schluss ziehen, dass die Labyrinthe den Verlauf der Starre der quergestreiften Muskeln beeinflussen. . . . Doch soviel geht mit Sicherheit aus dem Versuchen hervor, dass jedes beiden Labyrinthe die Starre der Muskeln, mit denen es enger zusammenhängt, beschleunigt." He also discovered (*568*) that if the labyrinth of an animal is injured and then the animal is killed, the usual *rigor mortis* does not, in most cases, occur; a result also confirmed by Sherrington (*1423*, pp. 338 ff.) Ewald believes that many of the facts observed as peculiar to aural stimulation are caused by a lack of tonicity and innervation. That is to say, the ear is not wholly a compensatory organ. Sherrington (*1423*) likens the canals to the proprioceptive organs of other parts of the body, but supposes that whereas these latter give only local reflexes, the canals, because of their position in the head-segment, give tonic excitations to the musculature of the whole body in the maintenance of attitude. Numerous other tonic effects have also been described. Scott (*1399*)

[44] See also Cyon (*478*, p. 38.)

found that the extirpation of one labyrinth produced effects upon the resting state as well as upon the movements of the animal. Ziba (*1698*) and Güttich (*711*) have considered the probability that death fom cold shock during swimming may be referable to want of tonic control of the organism during thermal stimulation of the canals. The work of Camis (*386-392*) suggests that the relations obtaining between the canals and the rest of the body, whether for the maintenance of tonus or for widespread glandular and muscular effects, is far more intimate than has as yet been demonstrated. Other writers have spoken of "Muskeltonus" (*1619*) or of "tonische Reflexe" (*1586*). Allers (*48*) has given an elaborate summary of pathological material contributing to the notion of the canals as tonic organs. Ach (*4*), Alder (*6*), Benedicenti (*197*), Bickel (*228*), Crocq (*435, 436*), Dreyfus (*532, 533*), Hartenburg (*726*), Jendrassik (*824*), Langelaan (*943, 944*), Lewandowsky (*974*), Magnus and Kleijn (*1042-1044*), Marcan (*1059*), Marikowsky (*1064*), Moscucci (*1133*), Shambaugh (*1419*), Sonntag (*1434*), Trendelenberg (*1543*), Tschirjew(*1554*), Verworn (*1586*), Weinland (*1619*), and especially Jaeder holm (*821*) have also found the end-organs in the canals to be organs for the maintenance of muscular tonicity.

4. *Compensatory.* The term "compensatory movements" introduces a more specific function of the canals than any we have yet found. It suggests that the canals are organs for keeping the body oriented or compensated to displacements in position. We have already seen that there was at first some difference in opinion as to whether the effects of stimulating the canals were the result of positive reflex innervations or whether they were the result of an absence of tonic control. From either point of view, however, it must have been noted that the movements made were almost always compensatory. That is to say, the animal seemed to be endeavoring to maintain its usual normal attitude against an invisible disturbance. We have pointed out, furthermore, that the ocular effects of ampullar disturbance are usually the most definite and most easily observed of all the effects induced. We find, therefore, that compensation has come to be closely related to eye movements. Our chief concern is with compensatory movements of the eyes that are obviously vestibular, however, and not with the compensation measured by Contejean and Delmas (*427*), Mulder (*1141*), Nagel (*1163, 1164*) and others when the body or the head is tilted to one side or the other.

Crum Brown (*442*) was at least one of the first to suggest that

the movements made after sectioning a canal were the result of an effort on the part of the organism to preserve the same position. He has given, furthermore, a full description illustrated with drawings of the alleged ocular compensations resulting from vestibular stimulation. Since Crum Brown, the use of the term "compensatory" has been frequent and more recently the excellent studies of Lyon (*1012*) and Maxwell (*1091*) have demonstrated that the movements resulting from ampullar stimulation are for the purpose of keeping the organism adjusted under disturbance.

Fridenberg (*617*, pp. 161 ff.) has suggested another sense in which the movements which we have been discussing may be called compensatory. He has, for example, pointed out the similarity between the relatively simple somatic reactions of the lower animals called tropisms and the movements resulting from excitation of the end-organs in the canals. In this manner "the varied changes of attitude and position can all be reduced teleologically to a simple formula or principle, the gist of which is that a final optimum of position is secured for the organism." With increase in complexity of structure these somatic reactions or compensations become more accurate and delicate and finally become characterized as static and dynamic functions.

In addition to these empirical theories concerning the canals, we have already referred to certain philosophical speculations regarding their function. Cyon, it will be remembered, found within the canals the end-organs underlying the concepts of space, time and number. The canals have, furthermore, been considered by Chapman (*404*) and Viguier (*1588*, *1589*),[45] as a mysterious organ for the sense of direction. Alix (*45*), Ayres (*67*), Brown (*329*), Cholande (*408*), Clararède (*410-411*), Güttich (*712*), and Velden (*1583*), have also contributed to this theory. In the light of the work done on thermal means of exciting the ear and of the facts pointed out by Ewald and others, it does not seem out of place to suggest that seasonal differences in temperature either in the air or the water may be an adequate stimulus to the semicircular canals or to the lateral line organs for the release of certain tonic sets that may account for the

[45] ". . . Je crois avoir enoncé le premier, il y a cinq ans déjà, la théorie qui attribute principalement à des notions fournies par les canaux semi-circulaires la faculté possédee par beaucoup d'animaux, et même par certains hommes de revenir directement à leur point de depart après des detours multiplies en pays inconnu." (*1589*), p. 868).

migratory passage of birds and fish. The supposition that these organs act according to some of the ways that have been suggested by common sense takes us back to the days of magic and not to the days of scientific observation.

5. *Summary and conclusion.* It appears, then, from the facts that have been submitted that the ear contains a mechanism which is adapted to maintain the position of the body in space, to make it cognizant of translational and of rotational movements, to keep it in a constant state of tonicity, and, finally, to enable it to compensate, by appropriate movements, changes that may occur in its position. To what extent these four functions overlap is another matter. It is probable that the perception of verticality or of position is conditioned in part, at least, by the set of the muscles at any given moment. It is furthermore probable that the cognizance taken of rotation or of translation is not direct, by way of unique mental processes, but indirect, and by way of compensatory movements with the attending kinaesthesis and organic sensation. At any rate, it does appear that the nonacoustic portions of the ear are functionally related to tonus and to compensation.

E. *The Central Connections of the Receptor.*

One cannot read very far into the literature on vestibular and cerebellar neurology without involuntarily warning one's self against a danger into which this branch of neurology has apparently run headlong. The analogy of the telephone exchange has been so easily drawn and the reflex arc concept has been so illuminating that we are threatened with a piecemeal neurology instead of a picture of an integrating and coordinating mechanism. The recent neuro-otologists especially have been under the instruction that they were to pick out isolated neural tracts and relate them in a definite fashion to the equilibratory mechanism.

1. *With the cerebellum.* It is beyond the scope of this investigation to point out in more than a very general way the probable central connections of the vestibular branch of the VIIIth nerve, the branch which has its terminus in the ampullae of the canals and in the saccule and utricle.[46] So far as we are here concerned, it is sufficient

[46]For more detailed descriptions the reader is referred to Cajal (*382, 383*), Golgi (*665*), Van Gehuchten (*646*), Cameron and Milligan (*384, 385*), Holmes (*780a*), Scott (*1399*), Matte (*1084*), Leidler (*964, 966*), Mills and Jones (*1118*), Retzius (*1302*), Biehl (*230*), Voit (*1594*), Thomas (*1529, 1530, 1531*), Bárány and Wittmaack (*144*, pp. 38 ff.), Winkler (*1643, 1644*), Streeter (*1504*), Bonnier (*261*), and Wilson (*1632*),

to note that the vestibular portion of the VIIIth nerve enters the medulla oblongata immediately behind the pons and terminates in a vestibular nucleus which forms an eminence on the floor of the fourth ventricle. Through this nucleus the inner ear is connected with the medulla for local bulbar reflexes, with a spinal tract for movements of the trunk, limbs, and head, and with the mid-brain for movements of the eyes. For our purposes, the significent fact is that "there is no important pathway from the vestibular nucleus to the thalamus and cerebral cortex. . . ." (Herrick *757*, pp. 184, 186). The functions carried out by the canals are thus completed without the neural means for a specific mental correlate. On the other hand, the fact that the cerebellum is, genetically regarded, a suprasegmental outgrowth of a vestibular nucleus and that it has come to act as an overlord over the proprioceptive functions of the body suggests that the mental consequents of vestibular disturbance are all indirect and secondary. As has been demonstrated by numerous writers, the anatomical and functional relations obtaining between the semicircular canals and the cerebellum are exceedingly close. Excitations running into the cerebellum are then relayed, apparently, to muscle groups all over the body and so maintain the tonus or initiate the compensatory movements that have been so frequently described. The exact character of the relation between the canals and the somatic mechanisms may be discovered in a large number of papers by such men as Clarke and Horsely (*417*), Koranyi and Loeb (*896*), Kron (*912*), Lange (*942*), Lewandowsky (*975*), Luciani (*1001-1004*), Munk (*1148*), Onimus (*1189*), Pagano (*1193*), Podmaniczky (*1240*), Probst (*1254*), Pros (*1255*), Rynbeck (*1314*), Russell (*1347*), Schiff (*1376*), Schklarewsky (*1384, 1385*), Sergi (*1404, 1405*), Stefani (*1450, 1452, 1454*), Thomas (*1529*), Thornval (*1534*), and Verzilov (*1587*).

2. *With the somatic effector-organs.* The semicircular canals have, apparently, no connections running directly to the trunk. That is to say, every excitation passes, apparently, through the cerebellum. Many attempts have been made, however, to trace specific pathways through the cerebellum and as far as specific effector organs. If we may rely upon the facts that have been offered the neural connections between the semicircular canals and the body are more specific than they have been supposed. Güttich (*713*), for example, sought to relate cutaneous temperatures with the semicircular canals,

and Fano and Massini (*580*), demonstrated certain functional relations obtaining between the canals and the respiratory system. We have already referred (Camis, *386-392*) to the influence which the vestibular apparatus may have on the vascular and glandular systems. Marikowsky (*1064*) has sought a still more definite statement of the muscular connections of the labyrinth. One of the principal tasks has been the discovery of the neural pathways from the ear to the ocular muscles. Numerous investigators have committed themselves to this problem, among whom are Wilson (*1632*), Wilson and Pike (*1634*, *1639*), Cyon (*454*) and especially Högyes (*786*, *787*, *788*). The attempt has also been made by Bartels (*154*, *156*, *157*, *158*), Bartels and Ziba (*159*), Wilson and Pike (*1631*, *1638*), and Ivy (*817*) to localize the cerebral centers for the fast and slow components of the ocular movements, but the matter seems to await further experimental evidence. A few facts concerning the central neurology underlying compensatory movements have been gotten direct from the clinical laboratory by observing the degeneration of certain tracts following aural disease or surgical operation. Deganello (*492-495*), Ferrier and Turner (*585*), Meyer (*1112*), Pelizzi (*1215*), Zange (*1691*, *1692*), and Soprano (*1437-1440*), have done good work on this problem. Of the evidence from the method of rotation we shall speak later. (See below, pp. 51 ff). Retjo (*1296*) has searched for the neural conditions of the quiet phase of vestibular nystagmus, and Pike (*1233*) has devoted one paper to a search for the nervous conditions of the rapid phase. Other studies on cerebellar localization have been made by Guggenheim (*707*), Henri and Stodel (*748*), Hoffman (*778*), Ivy (*817*), Kohnstamm (*886*), Leidler (*966*), Marburg (*1058*), and Muchens (*1156*, *1157*). Finally, considerable attention has been given more recently to the structure and distribution of the end-fibres of the vestibular branch of the VIIIth nerve. Bielschowsky (*168*) and Kolmer (*888*, *889*) have been pioneers in this field. Wenig (*1623*) has also added much to our knowledge of the terminal structures. At the present state of our knowledge, too much importance cannot be attached to the tracing of fibres through the central nervous system. The task is, of course, enormous, and the achievement of investigators is encouraging, but adolescence is frequently apt to color too highly its observations.

3. *Summary and conclusion.* The facts seem to show that the more gross central connections of the vestibular portion of the

VIIIth nerve are fairly well established. These facts make it clear that the canals are structurally connected through the cerebellum with all parts of the bodily musculature and that, therefore, they are in a position to play a large part in the maintenance of bodily posture as well as to maintain muscular tonus.

F. *The History of the Receptor.*

Deductions from ontogenetic and phylogenetic accounts of life and mind have become popular in recent years. Some of the facts thus gained are extremely suggestive and others are but indifferent. On the whole, however, the genetic method has been extremely valuable in the sciences of life, and developmental studies upon the ear have been an important source of information regarding the probable functions of the semicircular canals and related equilibratory structures. The first problem in the genetic group has been the attempt to relate the semicircular canals to the lateral line canals of fishes. Some attempts have even been made to run back as far as the air bladders among lower organisms, and finally to certain geotropic tendencies on the part of unicellular animals. From the facts submitted, however, it is not altogether clear that the lateral line canals are equilibratory end-organs. The second problem of the genetic group has been to depict typical equilibratory end-organs at various stages of animal evolution. This problem falls, in part, as we have seen under the discussion of comparative anatomy. It is not within the scope of this survey to refer in detail to the ontogenetic and phylogenetic facts as they appear in the literature. The experimental studies are fairly numerous, however, as may be seen by referring to Clapp (*412*, *413*), Doran (*530*), Fick (*586*), Fleissig (*596*), Franz (*609*), Fuchs (*633*), Hamlyn-Harris (*722*), Harrison (*725*), Hartridge (*729*), Heilig (*741*), Ilyin (*813-815*), Jenkins (*825*), Johnson (*830*), Kettel (*862*), Landaere and Conger (*936*), Lee (*958*, *959*), Lyon (*1013*), Maday (*1032*), Malbranc (*1047*), Marage (*1055*, *1056*), Moodie (*1124*, *1125*), Moser (*1134*), Murbach (*1153*), Netto (*1169*), Nicolle and Comte (*1176*), Noorden (*1179*), Ostwald (*1192*), Parker (*1206-1208*), Patten (*1214*), Prentiss (*1249*), Quix (*1265*), Rabinowitsch (*1271*), Reisinger (*1294*), Ridgewood (*1312*), Rüdinger (*1340-1342*), Sargent (*1364*), Schäfer (*1374*), Schultze (*1393*), Sewell (*1406*), Shambaugh (*1421*), Sorensen (*1441*), Stauffacher (*1448*), Steiner (*1480*, *1482*), Thienemann (*1527*), Thompson (*1533*) and Tullberg (*1556*).

G. *Recent Clinical Methods and Results.*

The recent history of the functions of the semicircular canals has been written for the most part in the clinical laboratory. The interest of medical men has been equally divided between two different undertakings. On the one hand lay the task of interpreting in the light of the physiological facts the large amount of pathological evidence regarding the functions of the canals; and on the other hand stood the problem of making diagnostic use of the facts already known. It was essential that the facts regarding equilibration and its disturbances be turned to account in the treatment of a variety of aural disorders.

1. *The contributions of pathology.* We have had occasion (p. 15 above) to refer to the disappearance of vertigo following pathological exudation of the internal ear. (Toynbee, *1540*, *1541*). This is a good example of many pathological occurrences that have from time to time attracted the attention of doctors and of scientific men. In 1861, Ménière drew, on the basis of Flourens' work, a clinical picture of the now familiar symptoms of vestibular impairment or destruction, a picture which has since been known as 'Ménière's disease.'[47] We have shown, it will be remembered, that the first step of importance in determining the functions of the canals was the demonstration that the same effects resulted from aural stimulation, from sectioning the vestibular portion of the VIIIth nerve, and from cerebellar destruction. It was of great importance, therefore, to note that pathological ears were usually found in conjunction with the same general defects of behavior. The significance of this discovery was not appreciated, however, until after 1898, when, at the Otological Congress in Moscow, Jansen gave a paper detailing ten operative cases on the human labyrinth. Modern clinical interest in the subject is said to derive from this paper (see Scott, 1399). Within a few years, the clinical laboratory has furnished a good deal of evidence to show that the canals as well as certain central nervous structures are closely related to disturbances of equilibrium. Pathological cases have always been considered by science as a contribution of material from Nature's larger laboratories. The value of such evidence was fully appreciated by Crum Brown, as we have seen. In addition to anticipating the work of James (see above p. 17), he reported a case of pathological vertigo occurring in himself with the hope of gaining further knowledge about the canals (*442a*).

[47] *Cf.* Gould (*671*).

Although as late as 1900, M'Kendrick and Gray complain that the "light thrown upon the subject by pathological evidence is scanty," nevertheless, since that time, such evidence has increased at an amazing rate. A group of Viennese clinicians[48] have been especially active in tracing the significance of pathological disturbances, while in this country Friesner and Braun (*307*, *628*) illustrate the nature of the work that has been done. A few of the more important papers on vestibular and cerebellar pathology have been written by Borovikov (*288*), Carpenter (*396*), Cohn (*422*), Egger (*549*, *551*), Grasset (*683*, *684*), Haug (*736*), Herzfeld (*763*), Kano (*848*, *849*), Krotoschiner (*914*, *915*), Leidler (*963*), Lucae (*1000*), Lussana (*1007*, *1008*), Mackenzie (*1025*), Matte (*1086*), Mauthner (*1089*), McBride (*1096*), Ménière (*1110*), Moos (*1128*), Munk (*1147*), Münter (*1151*), Muratov (*1152*), Mygind (*1159-1161*), Nager (*1167*), Oppikofer (*1191*), Pike (*1234*, *1235*), Puglia (*1256*), Rhese (*1306*), Richter (*1311*), Ruttin (*1350-1355*), Scholtz (*1390*), Sewell (*1408*), Shambaugh (*1411*, *1420*), Stein, C., (*1455*), Stein, S., (*1459-60*; *1463-1464*; *1468-1474*; *1475*), Török (*1539*), Trifiletti (*1549*), Urbantschitsch (*1575*), Wittmaack (*1652*, *1653*), Woakes (*1661*), Yearsley (*1685*), Zange (*1691-1693*), and Zeroni (*1696*).

Not the least important part of the contribution made by the clinical laboratory falls under pathological anatomy. By means of such studies the chapter on vestibular anatomy has been brought to a higher level than any other chapter recounting vestibular research. Haug (*735*), Klug (*874*, *875*), Knick (*878*), Lagally (*935*), Lucae (*997*), Marx (*1071*), Mygind (*1188*), Panse (*1202*, *1203*), Ruttin (*1352*), Schwabach (*1395*), Voltolini (*1600*, *1601*), and Wittmaack (*1651*) have made serious contributions toward the solution of this problem.

2. *The Clinical Tests of Normality.* The second problem of the clinician in otology was to make over the facts concerning the canals and their relations to equilibrium in such a way that they could be used as quantitative measures of function. Now the history of science has repeatedly shown that after a more or less substantial body of fact has been gathered together the urge of practical application usually becomes insistent and dominating. Usually two courses will appear. The demand for application will either suggest problems that need to be solved, not only to the advantage

[48] *Cf.* Bibliography for papers by Bárány, Ruttin, Alexander, and Höyges.

of applied science but to that of pure science as well, or the effort to make practical use of the material on hand will lead to a hasty generalization of the facts, an uncritical use of the generalizations, and a resulting confusion of the scientific issues. The history of the vestibular functions is a case in point for recent interest in the subject has centered almost wholly in the clinical laboratory. On the one hand, the clinician has been implored to furnish a means of relief from vertigo and from cerebellar tumors and lesions; on the other hand, the idea has become prevalent that all the facts regarding the equilibratory mechanisms have been discovered. By referring to the titles appearing in successive five year periods it will be seen that scientific or experimental interest in the canals was almost at its lowest at about the time the clinical interest became dominant.

About 1900, Robert Bárány, an aural pathologist of Vienna, came upon the growing tradition that the canals are closely associated by means of certain neural connections with the whole musculature of the body for the apparent purpose of contributing to the maintenance of bodily equilibrium. He found, as many others had, that whenever the canals were excited definite effects were produced, the most obvious and constant of which were the ocular movements. On the other hand, he was aware that the pathological laboratories had accumulated numerous cases of equilibratory and cerebellar diseases which were not apparent until so far advanced as to be fatal. The brilliant idea came to Bárány of using the ocular responses as an index of the functional integrity of the neural mechanisms involved in equilibration. Bárány (*98*, pp. 198 ff.) set to work on ocular movements and distinguished at least ten different kinds which might be called nystagmus movements. He selected for his primary consideration those known as vestibular nystagmus.

Ocular movements and especially those following excitation of the canals had already received widespread attention. Bárány's achievement lay, then, not in his description of vestibular nystagmus but in the use to which he put it. The facts regarding these eye-movements had already been pretty well established by 1900; and vigorous discussion of them has continued periodically from then until now. Brose (*328*), Buys and Coppez (*377*), Court (*433*), Czyharz (*483*), Frey and Hammerschlaag (*614*, *615*), Grain (*679*), Igerscheimer (*811*), Kelley (*859*), Kobrak (*882*), Koranyi (*894*), Kubo (*916*, *917*), Lémaitre and Halphen (*967*), Lemere (*968*), Lourié (*993*), Maas (*1014*), Nieden (*1177*), Nochte (*1178*), Oglesby (*1184*),

Peschardt (*1216*), Pflüger (*1221*), Reid (*1290*), Rodger (*1317*), Schwabach (*1394*), Simon (*1429*), Skrebitsky (*1431*), Stähli (*1447*), Stcherbak (*1449*), Wilbrand (*1678*), Wirths (*1648*) have made the most serious contributions to the subject of vestibular nystagmus.

Many clever means have been devised for measuring ocular movements aroused during rotation and under certain other conditions. These means have been devised, for the most part, by Angier (*54*), Bárány (*122*), Buys (*364-368*), Grim (*700*), Kiproff (*867*), Kobrak (*884*), Koch (*885*), Rothfeld (*1332*), Schackwitz (*1368*), Stein (*1458*), Tanturri (*1523*), Tuyl (*1565*), Uffenorde (*1570*), Verwey (*1584*), Vojacek (*1596, 1597*), Weber (*1613*), Wichodzew (*1627*), and Zalewski (*1689*). None have worked as seriously and cleverly, however, as have Dodge (*522-525*), Holt (*781, 782, 783*) and other psychologists.

Bárány entered upon a series of investigations upon the subject of aural pathology which, in 1913, won him a prize from the Society of German Otologists, and in 1915, the Nobel prize. His first significant paper (*96*) was the result of some twelve years of work upon more than 200 subjects, 33 of whom were deaf and dumb.[49] Although his work has received a great deal of attention, it is only fair to say that his principal contribution has been the reorganization of the facts so that they could be used in the clinical laboratory. He is heavily indebted to many of the men whom we have already discussed and especially to Ewald and to Höyges and Ruttin, drawing largely from them by way of quotation and other material. A coworker has given the following judicious estimation of his accomplishments: "Trotzdem muss es das unbestrittene Verdienst Bárány's bleiben, die groszte Bedeutung der vom Vestibularapparat auszulösenden Reaktionen für unsere klinische Diagnostik erkannt zu haben und vor allem durch systematisches Studium dieser Reaktionen am Menschen unter Heranziehung einer neuen bisher ganz ungebrauchlichen Erregungsart (der kalorischen Erregung) klinische Untersuchungsmethoden des Vestibularapparates ausgearbeitet zu haben, die als ein ganz wesentlicher Fortschritt in der Erkennung der Labyrinthleiden und in der Deutung der von ihnen oder zugehörigen nervenbahnen angehorden Symptome anzushehn ist."[50] He standardized four of the traditional methods of exciting the canals and, by applying them to both normal and pathological cases, he

[49]See (*96-144*) for the list of subsequent papers by Bárány.
[50]Wittmaack (*144*, p. 76).

soon developed a group of indices for normality that created a profound impression in otological circles. For example, he measured the time of the after-nystagmus and its direction and found, in confirmation of many previous observations, that the direction of the nystagmus was related to the direction of the alleged flow of liquid in the canals. By taking account, therefore, of the time of nystagmus and of its direction, and having in mind the central connections for the various ocular movements, he and others of the Viennese school[51] of otologists succeeded in diagnosing the place and and extent of cerebellar and other central lesions. The ability to make a practical diagnosis rested fundamentally upon a series of 'normality tests' formulated by Bárány. Of the three chief tests, one depended upon the ocular movements and two upon the grosser movements of the limbs. We shall be primarily interested in the first, the alleged 'nystagmus test.' Here especially the therapeutical and professional interests of the otologist have led toward strained and doubtful interpretations of the experimental facts. Instead of using his generalizations as a means to further scientific inquiry, the otologist has proceeded to announce for the sake of clinical diagnosis, a doctrine of the nature of nystagmus and of the other effects of rotation which is not a little questionable.[52] We have already seen that a great deal of evidence supports the assumption that the canals are chiefly concerned in disturbances of equilibrium. It was pointed out, however, that this kind of evidence does not prove that the canals are *principally* concerned in the perception of rotation or of disturbances of equilibrium. It is one thing to point out—as does Herrick[53]—that the canals are instrumental in the maintenance of equilibrium but quite a different thing to maintain that they alone are concerned in, or that they make an essential contribution to, the perception of rotation. Now the otologists have failed to make

[51]Neumann, Höyges, Alexander, Ruttin, and Bárány are commonly spoken of as belonging to the Viennese school. Neumann has been principally interested in clinical studies, while Alexander is a professor of anatomy.

[52]In certain directions, American otologists have gone further than the Austrians. Bárány's work is the natural culmination of the work that had been done before him. But the American otologists have been inclined to take the more prominent features from Bárány's work and used them in an uncritical manner, missing the significance in the historical setting. Furthermore, they have not always observed the distinction between a recital of the conditions under which facts are given and an inquiry into the facts themselves.

[53]His statement, "The semicircular canals are the most highly specialized organs of the proprioceptive series, and are chiefly concerned with the maintenance of bodily equilibrium," (757, p. 183) does by no means imply that the maintenance of bodily equilibrium is accomplished chiefly by the canals.

this distinction. They have accepted the theory that the canals are the sole end-organs, not only for the maintenance of equilibrium but for the arousal of the appropriate mental qualities. They have applied, in an uncritical way, the principle of inertia to the flow of the liquid in the canals and have definitely related the direction of movement of the liquid to the direction of the resulting ocular movements.[54] The relation of the direction of eye-movements to the theoretical flow of liquid in the canals, has, of course, been known for many years.[55] Cyon, it will be recalled, produced ocular nystagmus by opening the horizontal canals in pigeons and rabbits and blowing into the canal. Ewald used a compression and rarefaction syringe. Both of these men pointed out the fact, which has since become a rule, that the eyes deviate in the same direction as the assumed flow of the liquid. Attempts have also been made to show that head movements are subject to the same rule. In describing the central connections of the equilibratory end-organ the otologists have again gone beyond the facts. With the development of the concept of the reflex arc[56] it has been easy to make the mistake of supposing that the whole nervous system is composed of separate and distinct neural arcs which independently carry out their unique functions, unless perchance *as arcs* they are united to some temporary end. Long ago the hypothetical "faculties" of phrenology were driven by the psychologist out of the cerebrum; but the otologists are still seeking to habilitate them in the medulla and the cerebellum. They have created a neurology of the central connections of the vestibular nerve that is amazing in its theoretical detail. Höyges (*786*, *787*, *788*)—as an instance— has sought to differentiate twelve ampullar nerve-endings and to correlate them, one by one, through the central system, with the twelve eye-muscles; and Jones (*839*) furnishes a still more interesting example of the fabrication of a neural mechanism suitable for the otological clinic from a few facts and a generous amount of theory. Finally, the otologists have failed to consider

[54]See Bárány and Wittmaack (*144*, pp. 84-116) for a discussion of the mechanics of exciting the ampullar end-organs.

[55]Certain American otologists have accepted quite naively the theory that there is a perceptible flow of liquid in the canals. For example, "When an individual is turned, be it in the laboratory or in an aeroplane, there is produced a circulation of this fluid (the endolymph) in certain definite canals and planes. Now, if the turning is suddenly stopped, or if the aeroplane comes out of a rotating maneuver, the fluid in the canals continues to move in its former plane by sheer force of its momentum." Fisher and Lyman (*593*, p. 1979); *cf.* Babcock (*71*, pp. 346.)

[56]See Gault (*645*) for an account of the development of the concept of the reflex arc.

that all the facts about the canals that were at their disposal rested upon an observation of the initial effects of unrepeated ampullar stimulation. This failure on the part of the clinicians is probably the secret of their whole difficulty. It does not seem to have occurred to any experimenter that the effects of vestibular excitation might be modified in kind and in intensity under the changes in the condition of arousal. Some writers, it must be admitted, have pointed out that nystagmus may be modified under certain conditions. No one, however, seems seriously to have considered the implications of this possibility. For example, Fridenberg (*623*, p. 1338) says: "A word of warning should be spoken as to accepting without modification the hard and fast rule as to an exact number of seconds of after-turning nystagmus to be elicited by passive rotation of the patient. Von Cyon and others noted long ago that this reaction, as well as the kindred phenomena of dizziness and falling sensations, depended largely on the patients' previous habits in turning, or reversing in dancing, by his being right or left-handed, etc., and that they were variously modified by these." Bárány (*98*, pp. 211, 217, 225) speaks of modifications of the time of nystagmus by variations in the mode of fixation and in the position of the head. He further says (*106*, p. 486) that dancers who continually turn in one direction have less nystagmus when rotated in the same direction, although if they usually whirl in both directions no decrease in nystagmus time can be discovered.[57] Bárány (*106*, p. 492) was, however,unable to find any change in duration with repeated turnings; but his series were not continued for any length of time. Wintermute (*1647*, p. 99) finds that normal reactions do not hold with ballet dancers when turned in the direction they are used to whirling. Abels (*1*, pp. 410 ff.), likewise, found some effect of repetition in doves. Parsons and Segar (*1209*) say that nystagmus is greatly decreased in aviators and whirling dancers. All of this is contrary to Fisher and Babcock who sought to "have it definitely settled once and for all that army aviators do not lose their nystagmus as a result of the rotation and whirling to which they are subjected" (*592*, p. 780). There is at least one reason for this strange neglect. We have seen that almost all of the early work on the vestibular mechanisms was done on animals, and, in most of these cases, the animal appears to have been so mutilated as

[57]See also McKenzie (*1102*, p. 65).

to preclude adequate observation on the influence of repeated experimental excitations. At any rate, the literature shows no evidence of a consistent description of the effect of repetition on the results of vestibular excitation. Under the circumstances, it is not strange, then, that the otologists proposed their central doctrine, *viz.*, that nystagmus is a simple and inevitable effect of ampullar stimulation and is isolated from all the other effects of such excitation. Our historical survey has, of course, emphasized repeatedly that the effects resulting from stimulation of the ears are sub-cortical and relatively direct. This is not to say, however, that the effects are simple reflexes. The writer has been unable to find that the original conception of Bárány and others of the Viennese School included this assumption. The American followers of Bárány, however, have made free use of the supposition. Jones (*839*, p. 187) says: "Ear stimulation causes a pulling of the eyes; this is easily understood as a simple reflex. . . . . This reflex exists by itself and has no part in the causation of past-pointing;" and Babcock (*70*, p. 347) repeats that "nystagmus, at least the slow component, is distinctly a reflex phenomena." In speaking of the tests based upon this supposition, Wintermute (*1647*, p. 97) says: "These tests are based upon the normal reflex reactions of the semicircular canals in producing nystagmus of the eyes." So also Wilbrand (*1628*, p. 583): "Diese thatsächlich vorhandenen, von dem Willen unabhängigen Bewegungen, können nun keine anderen, als reflektische Bewegungen sein." Also Stone (*1503*, p. 212): "Such stimuli produce in normal cases, fixed and unchanging reactions, *i. e.*, definite forms of nystagmus, vertigo, and past-pointing (armataxia) depending upon the strength and duration of the stimulus and the point of application.[58] The conception is, of course, important, if it is true. If nystagmus is a simple reflex, the otologists are quite right in claiming that repetition will not permanently affect it. The work of Pawlow, indeed, does suggest that reflexes may be modified; but here we are dealing with a different matter. The simple reflex conception was one that admirably served the clinicians purposes. It was only necessary to describe the central path of the neural arc involved and then to administer a 'test' in order either to determine the functional integrity of the arc or to discover the seat of a lesion. The scheme was beautiful in theory and it has seemed to work fairly

[58]See also Shambaugh (*1410*) and Fisher and Babcock (*592*).

well in otological practice; although one cannot be sure that the otologist has not been counting hits and neglecting misses. He has maintained that the seat of a central lesion in the pathways in question could be divined from variations in the time or in the nature of the ocular responses following aural stimulation. He has stated, furthermore, that the normal after-nystagmus for a rotation-period consisting of ten revolutions in twenty seconds should continue more than 15 and less than 35 seconds. There is, however, nothing sacred about these times; although the procedures of the otologist would point to that belief. Bárány (*106*, p. 497) thought he found that optimal effects are obtained in about ten revolutions in twenty seconds and it has become customary, therefore, to use these values in diagnostic and descriptive work. Times materially above or below these amounts indicated to Bárány a pathological condition of the ears or of the cerebellar structures.

Bárány's tests have given rise to a large literature directly relating to his own work and to diagnostic methods in general. More recently the experimental and clinical literature has centered about the tests for "normality" given to prospective candidates for the Army air service. Bioch (*237*), Björkman (*238*), Blohmke and Reichmann (*246*), Blumenthal (*247*), Coulon (*432*), Dighton (*520*), Friedman (*625*), Grivat and Rigaud (*701*), Guthrie (*709*), Halphen (*720*), Hastings (*734*), Hautant (*738*), Langdon and Jones (*941*), Lautmann (*953*, *954*), McKenzie (*1101*), Norgenroth (*1180*), Parsons and Segar (*1209*), Pfister (*1220*), Rothmann (*1336*), Sewell (*1407*), Shambaugh (*1410*), Shinkle (*1426*), Sonntag and Wolff (*1436*), Stenger (*1488*, *1489*), Stone (*1503*), Tabor (*1522*), Thacker (*1526*), Trible (*1548*), and Tweedie (*1565*) have discussed the Bárány tests. General diagnostic methods which relate more or less directly to Bárány have had the attention of Bezold (*221*), Carpenter (*345*), Chamberlain (*403*), Doehne (*526*), Duel (*536*), Dufour (*537*), Gatscher (*644*), Gower (*672*), Graef (*678*), Hayman (*739*), Herzfeld (*762*), Hinsberg (*767*), Kerangel (*860*), Kerrison (*861*), Knoll (*879*), Kobrak (*881*, *882*), Lang (*939*, *940*), Lermoyez and Hautant (*971*), Levy (*972*), Lewis (*978*), Mackenzie (*1023*, *1024*, *1026-1029*, *1031*), Mann (*1051*), Maupétit (*1088*), Mills and Jones (*1117*, *1118*), Mollison (*1122*), Moure (*1137*, *1138*), Moure and Cauzard (*1139*), Müller (*1145*), Neumann (*1171*, *1173*, *1175*), Panse (*1201*, *1204*), Pfingston (*1219*), Rhese (*1307*), Rohardt (*1319*), Rosenfeld (*1325*), Rutlin (*1349*, *1356*), and Stein (*1476*). The Bárány tests and other similar

diagnostic methods have been applied directly to problems of aviation by Burtt (*360*), Cruchet and Moulinier (*438*), Foy (*605*), Germelli, Tessier and Galli (*649*), Head (*740*), Hunter (*799, 800*), Johnson (*829*), Juarros (*843*), Kronfeld (*913*), Lacroix (*929, 930*), Lewis (*980*), Lewis and Pike (*981*), Maublanc and Ratié (*1087*), Okovneff (*1188*), Piéron (*1226*), Robertson (*1316*), Small (*1432*), Stern (*1490*), Streit (*1516*) and Vincent.

Now the absurdity of making universal application of these tests did not become apparent until the time came to apply them to individuals who were normal and yet who had had long previous practice in rotation. That is to say, a man who had successfully travelled hundreds of hours in the air must be deemed "pathologic" if his time of after-nystagmus had notably decreased or disappeared. It has been shown, however, that after-nystagmus may decrease in just this manner and it is here, then, that the otologists have gone astray. In the first place, they devised tests based upon a partial knowledge of the facts. That is to say, they failed to consider seriously the possibility that nystagmus could be modified in supposedly 'normal' subjects. They insisted that "the average normal whose nystagmus time when not fatigued is approximately 24 to 26 seconds is the man who is physically most suitable for flying training." We have, therefore, the curious situation described by Fridenberg. "As normal labyrinths merely support the possibility of vertigo and false sensations of direction and space (past-pointing and falling) one might even venture the paradox that the safest aviators would be those with dead labyrinths." Even Fisher and Lyman mention the fact that vertigo is very confusing and often leads to disaster—aviators suddenly getting dizzy—but they further insist that "we must never think of immunity as leading to safety." That is to say, we find, according to the otologists, that the successful and safe flier is the one who comes out of a spin with his visual field so confused by the resulting ocular movements (not to mention all the other distressing effects of turning) that he must escape destruction only by a miracle. In the second place, the otologists did not take account of the sensitivity of the effects of rotation to changes in the conditions of arousal. They tested their experienced fliers, for example, by rotating them in the Bárány chair. Now it is difficult to see how they can justly contend that the conditions obtaining are the same. The axis of rotation is different, the rate different, the

spin effect varies, and, more important than all, the whole emotional and voluntary setting is different. For example, it has been found that pressing the feet against a support during rotation—as the aviator does with his rudder,—leads to a change in the psychophysical determination that may profoundly modify the effects of rotation. To test an experienced aviator in a rotating chair is inconclusive unless sufficient repetitions are given to determine the subsequent course of the nystagmus. We have found a decided "transfer effect." The failure of the otologists to consider the effect of a change in the conditions is reflected in their ill-advised attempt to explain a small decrease in nystagmus time in some of their experiments by supposing that their subjects had learned the trick of "gaze-fixing." They sought to eliminate this possibility by placing before the eyes of their subjects strong magnifying lenses. Now it has been demonstrated that, under these conditions, the time of nystagmus is increased so largely that it is difficult to see how any one could have failed to detect it. Nystagmus may entirely disappear in a subject who has fixated a point one meter away and yet be made to reappear when lenses are used. We have also found that if a subject turns his head in such a way as to keep the same field of vision before him as long as possible during rotation, almost no nystagmus will result One subject used became proficient in doing just this thing (a trick to which dancers resort in order to escape dizziness), and yet when rotated in the usual manner the subjest showed a long after-nystagmus. It must be emphasized, then, that the decrease in nystagmus—time is for one set of conditions only. The failure to recognize this fact has lead the otologists astray.[59]

A further difficulty must be considered. The ocular movements resulting from ampullar excitation are *not* isolated effects of rotation; they are a *part* of a complex and elaborate group of processes, bodily and mental.[60] Here again we are in conflict with certain otological dogmata. To separate nystagmus from the other effects of rotation, as the otologist do, is, however, just the thing one would expect to happen when the history of the subject is taken in an uncritical and undiscriminating manner. The ocular effects are almost always present. They often appear, especially in the human organism, in a manner that invites attention. On the contrary,

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[59]Manual (*1054*).
[60]See Griffith (*697, 698*).

other effects are not so apparent. Not all individuals become nauseated, and innervations of various parts of the body may be incipient only, failing to go over into overt movement. As a result, therefore, of this distinction between the ocular effects of rotation and the other effects, the otologists are put in the awkward situation of admitting that nystagmus is not modified by repetition while the other effects may be highly modified or may even disappear. A bias arising from the endeavor to protect the tests for vestibular normality is here clearly apparent. Now it is commonly known that individuals may with practice lose all 'sense' of vertigo. The otologists have been frank to accept this fact, but thereupon were put in the difficult place of showing why vertigo, past-pointing, and falling can and do decrease in intensity with practice while nystagmus does not so decrease. To quote: "The greatest usefulness of the knowledge that stunting is an ear problem lies in the fact that the flier may be educated to disregard the vertigo effects of his stunts in the laboratory instead of among the clouds, and without danger acquire a tolerance to a degree impossible in the air." Fisher and Lyman (*593*, p. 1978; Manual *1054*, p. 132). Or, one can "acquire in absolute safety a tolerance for the disturbing effects of vertigo induced by these revolutions." Manual (*1054* p. 133). Again: "The only final and really effective means of preventing seasickness is to get an individual accustomed to the extraordinary labyrinthine stimulation. The sailor and the seasoned traveler accomplish this by the many repetitions to which they subject themselves in their travels. We know, however, that it is not necessary to go out to sea in order to obtain the phenomena of labyrinthine stimulation. This can be easily accomplished in the turning chair. . . Such experimental stimulation should enable an individual to go aboard a ship for the first time practically a seasoned sailor. This thing has been borne out in our clinical experience in that repeated stimulation of the ears in the same individual has invariably shown an increasing tolerance." Jones (*839*, p. 45). Yet again: "All types of vertigo, no matter how induced, are made less and less disturbing by continual repetition." Fisher and Lyman (*593*, p. 1978). The other chief effects of rotation, *viz.*, past-pointing and falling were consequently described as objective signs of vertigo. According to Jones (*839*, p. 187), "The other reaction to ear stimulation is vertigo. It is not a reflex; it is a subjective disturbance of the cerebral cortex due to sensory impulses received directly from the ear. Pointing, on the other hand, is a cere-

bral motor act. Neither turning a person in a chair nor douching his ears causes him to past-point. He is asked to raise his arm then bring it back to find the finger. Before ear stimulation he is able to find the finger; after ear stimulation he is unable to find the finger because of the vertigo. It may be regarded as a law of the ear tests that where there is no vertigo there is no past-pointing. Vertigo is the primary reaction; past-pointing is a secondary manifestation." That is to say past-pointing is a voluntary "cerebral act." Now automatographic records taken during and after rotation prove that past-pointing and falling depend upon innervations as "involuntary" in character as is nystagmus. It is impossible, therefore, to interpret the accompanying vertigo and hence learn to recover the poise. "The whirling artists who spend years in professional whirling acts, when not fatigued show full normal responses to tests of their vestibular apparatus. Their art lies in the education and experience which they have gained and in the dexterity they have acquired in the repeated performance of their acts. For instance, a whirling dance may be creditably performed by a novice, but the professional whirling dancer will demonstrate his ability to stop dead still suddenly without a fall, whereas the novice will fall, because of the vertigo (or false sense of motion) he experiences as a result of his whirling. The difference between the artist and the novice lies in the artist's ability to place proper construction upon his false sense of motion, experience and education enabling him to estimate its degree of falsity so correctly that he is able to calculate his voluntary muscular control in a manner that results in his accomplishing a successful standing still. The novice, unpracticed and inexperienced in estimating vertigo, finds himself unable to do so successfully and falls to the floor." Manual (*1058*, p. 124). This is as pretty a bit of specious reasoning as ever adorned the pages of "research." A little knowledge is said to be a dangerous thing; but the most elementary knowledge of a "sense of motion," "dexterity," "voluntary muscular control," and other like matters which lie outside the province of the aural "specialist" would have served as a caution warning the writer against making himself ridiculous. We must insist again that the effects of rotation are an integrated group. We have found every member of the whole group to be equally modified by repetition and by other changes in the conditions of arousal. The logical separation made by the otologists leads them into the impossible position of admitting a modification of vertigo and falling and denying it to nystagmus.

3. *Summary and Conclusion.* We have found, then, that the chief interest of the clinical laboratory has been in the description of pathological cases of semicircular disturbance and in the promulgation of a series of tests for "vestibular normality." So far as pathology is concerned, we must conclude that the clinical description has contributed in some measure toward an understanding of the vestibular functions. The "normality tests," however, have been found to be based upon a questionable doctrine of the nature of nystagmus and of all the other effects of rotation. This questionable doctrine is apparently the outcome, in part, of a limited method of observation during the history of experimental work upon the subject, and, in part, of an uncritical interpretation of the facts and especially of the clinical work of Bárány.

H. *The Psychological Problem.*

The psychologist's primary task in the study of equilibrium is the description of the mental processes which are aroused by bodily rotation or by other means of excitation of the neural structures involved. Although the mental effects of rotation were among the first to attract attention, carrying us right back to the days of Erasmus Darwin and Purkinje, the psychologist's task has progressed but slowly. This is a striking fact; for it is obvious that the problem of equilibrium and of orientation are, in large measure, problems of mind.[61]

No problem falls more naturally to the psychologist than the analysis and description of the complex and baffling mental events involved in rotation. The slow progress is due, in part, to inherent difficulties, to the complexity and the high fusion of the mental processes involved and to the difficulties of observing under dizziness;[62] in part, to the fact that the experiences grossly observed failed to fit into

[61]Some of the recent medical writers have seemed to deny to the psychologists a legitimate interest in the problem. We read, for example, that "vertigo from whatever cause properly belongs in the domain of otology," and that "because of the anatomical relationships between the vestibular and the auditory organs, the problems of the canals should fall to the otologist." (See Carpenter, *395*, p. 899). With just as much reason, all the problems of hearing should also fall to the otologist, and with equal cogency the physicist might claim the whole field of sound or of vision, the chemist the whole field of smell and taste, and the alienist the whole domain of thought and emotion. The last half century of experimental psychology would seem to offer no excuse for such ignorance.

[62]See Titchener, (*1536*, p. 174).

the analytical rubrics furnished by the known departments of sense;[63] in part, again, to the doubt whether the vestibular portions of the inner ear contained a true organ of sense and so mediated specific mental processes; and, finally, also, to the fact that most of the work upon equilibrium has been undertaken by men equipped by their training for anatomical, physiological, and clinical investigations but unskilled in the analytical observation of mind. Alexander, (*29*, pp. 77-78) however, who has appreciated the fact that our lack of knowledge of the vestibular mechanism rests in part upon our lack of introspective knowledge, has stated the difficulties as follows: (a) It is as hard to distinguish the sensations arising from rotation from the muscle, skin, and joint qualities as it is to distinguish between gustatory and olfactory sensations;— (b) The vestibular nerve has no direct connections with the cerebrum and its functions are, therefore, largely subcortical; and (c) with the canals an undue excitation leads not to a change in quantitative values only as in the known sense-departments, but to apparently new qualities.

So it has come about that many of the hundreds of articles and books written upon our subject contain fragments and scraps of material which might be turned to psychological account, but which, taken either singly or all together, fail to give adequate or coherent information regarding the participation of mind in the striking disturbances of function which we have taken under our historical consideration. What we actually find, until we come down to recent times, is, for the most part, either casual references to "vertigo," "dizziness," and "confusion," or to such disturbances as the spinning of objects in the visual field and the feel of bodily qualms and discomforts. Sometimes the writers allude gravely to a "sense of motion," or to a "sense of equilibrium" or of "balance" without any critical or technical knowledge as to what a "sense" is and without inquiring whether there are involved in the functions of the semicircular canals and adjacent parts structures or organs which are designed to produce such specific processes of sensation as proceed from the stimulation of the eye, the cochlea, the skin, or the tongue.

1. *The emergence of the problem.* Let us briefly review the literature. The descriptions of Darwin (*488*) and of Purkinje (*1257-1261*) were given very largely in terms of the apparent movement of the visual field; although Purkinje did call attention to cer-

[63] See Külpe (*924*, pp. 140 ff) Murray (*1154*, pp. 390-395) etc.

tain organic changes. These he used to explain the facts of dizziness rather than as constituting the experience itself. Even 50 years later Crum Brown (*442*, p. 658) was unable to get beyond the behavior of objects. He says: "If we rotate about a vertical axis either actively (that is, turning ourselves) or passively (that is, being turned around on a movable chair or platform by an assistant) we are at first fully aware that we are turning and that external objects are at rest; gradually external objects seem to move around us in a sense opposite to that of our real motion. If at this stage we stop, we not only feel that we are being turned round in the opposite sense to that of the previous real motion, but we see, or think we see, external objects turning round. These two imaginary rotations, *viz.*, that of our body which we feel, and that of external objects which we see, take place about the same axis, in the same sense and at the same rate. The axis is parallel to the line in the head which was the axis of the original real rotation, and the sense is, as already explained, contrary to that of the original rotation." It is understood, of course, that our attention is devoted to what Brown (p. 449) calls "passive sensations of motion." There are whole masses of sensation localized in the musculature used to move ourselves about. These may be called "active sensations of motion," and they are not to be considered as dependent in any way upon vestibular stimulation. Neither is it sufficient that all of the sensations arising from rotation should be grouped together in a large mass, the whole being called "the sensation of rotation." When Crum Brown first attacked the problem of the canals (*439-441*) he took this course with reference to the mental events. "As far as I am aware, the sense of rotation has not hitherto been recognized either by physiologists or by psychologists as a distinct sense, but a little consideration and a few experiments seem to me to be enough to show that it really is so. By means of this sense we are able to determine—a, the axis about which rotation takes place; b, the direction of the rotation; and c, its rate. . . . In ordinary circumstances we do not wholly depend upon this sense for such information. Sight, hearing, touch, and the muscular sense assist us in determining the direction and amount of our motions of rotation, as well as of those of translation; but if we purposely deprive ourselves of such aids we find that we can still determine with considerable accuracy, the axis, the direction, and the rate of rotation." It is clear that Crum Brown has failed to distinguish, in this case, between sensations arising from the

inertia of the body and those arising from reflex innervations of the bodily musculature.

On the other hand, several investigators have taken more thorough account of the organic and kinaesthetic sensations aroused during rotation and have made much use of them. For example, Mach (*1018*, pp. 65-66) finds that of the mental processes involved in the perception of rotation the most important is that of vision which, combined with "skin-sensation" and "with changing innervations" yields "a conception of our body as in motion." "In passive movements of the body, reflex, unconscious innervations and movements of compensation make their appearance. In turning round to the right, for example, my skin sensation are connected with the same innervation as would be combined with the touching of objects in turning to the right. I feel myself turning to the right" (p. 66). Mach's first proposal of this thesis came in 1874 (*1016*). He was inclined to doubt that "special motor sensations exist which proceed from this apparatus (the canals, etc.,) as from a sense-organ," but that it simply "disengages innervations after the manner of reflexes" (p. 76). In another place he says: "the view is untenable that we arrive at knowledge of equilibration and of movement solely by means of the semicircular canals" (p. 74).

2. *Current problems and analyses.* By the time, then, that Mach and Brown had reached the conclusions we have just stated, the psychological problems had become fairly well defined. In the first place, there was an obvious need for a more accurate and searching analysis of the processes actually present during and after stimulation of the canals. In the second place, it was necessary to demonstrate under experimental conditions, either the existence or non-existence of a new mental element unique to the experience of dizziness.[64] Writers were continually positing such a quality by speaking uncritically of the "sensation of dizziness" or of a "swimming sensation." The otologists have, for the most part, displayed decided ignorance of psychological fact in their descriptions of the mental effects of rotation. Jones (*839*, p. 10) speaks, *e. g.*, of the equilibratory position of the ear as a seventh sense called the "kinetic-static sense." To quote: "any special sense depends upon an end-organ for the reception of stimuli, nerves to convey these stimuli and a nerve

[64] We have already pointed out (see pp. 33 ff.) the theoretical part played by the canals in ideas of space, time and number. We shall, therefore, not consider Cyon's theory here.

center to interpet their significance." The nerve center in this case gives an interpretation (!) called "vertigo." Vertigo, then, is a peculiar simple quality for the otologists. To quote again: "by vertigo is meant a subjective sensation of a disturbed relationship of one's own body to surrounding objects in space. It is not some general manifestation accompanying disorders of this, that or the other organ, but it is a disturbance perceived within a definite part of the brain, just as sight and hearing are perceived within the brain" (Jones *839*, p. 13)[45].

By referring to Brach (*302*), Busch (*363*), Graef (*677*), Guye (*714*, *715*), Herz (*766*, *761*), Hinton (*768*), Hitzig (*773*), Horsley (*795*), Hughlings-Jackson (*798*), Landois (*938*), Laségue (*945*), Linossier (*984*), Lussana (*1006*), Naumann (*1168*), Nothnagel (*1181*) Oppenheim (*1190*), Panse (*1198-1290*), Pacher (*1205*), Rhese (*1305*) Romberg (*1320*), Russell (*1345*, *1346*), Singer (*1430*), Stein (*1462-1477*), Steiner (*1483*), Stewart (*1498*), Stiebel (*1499*), Vaschide and Vurpas (*1582*), and Woakes (*1660*, *1661*), it will be seen that the otologists have been distressed for several decades by various phases of the problem of vertigo but by none so much as its purely mental aspect. Their long lasting difficulty lies, apparently, in their unwillingness or in their inability to put the experience of vertigo under severe laboratory conditions and to scrutinize it analytically.

Unfortunately, neither the problem of analysis nor the problem of the qualitative description of an alleged new mental element has received adequate treatment in the pyschological laboratory. Of the very few experimental studies, Holt (*783*) has undertaken the most serious. But of the three groups of processes contributing to the total perception of rotation, he finds but one that is essential, and this one group appears to be made up of nothing more or less than the *feeling* that either the body or objects about the body are in rotation. A good many other writers have stated that the perception of position and of motion is not a simple matter. Bourdon (*295*) says that all kinds of sensations enter into the complex perception of verticality. Fridenberg (*617*) gives the two following descriptions. "The adjustment of the individual to space, equilibrium, and the recognition of that adjustment, orientation, is, in man at least, a complex function. Touch and sight, muscle sense,

[45]See also Russell (*1345*).

in it widest meaning, sensations of pressure or tension, lightness or heaviness, in tendons, joints, and viscera, as well as the feelings produced by consciousness of changes of states of hyperaemia and anemia, all play a part" (p. 162). "The tactile sense, muscle sense, tonus and sensations in the viscera combine to form one large uniform source of sensations as to our position in space. Visual sensations, sensu strictiori and sensations of ocular muscle innervation, form a second. The third, labyrinthine sensations or disturbances are generally subconscious and for that reason externalized and interpreted by the sensorium as sensations of objective or subjective motion " (p. 199). The recent writers of psychological texts have treated the subject in the traditional manner. Descriptions of the canals and of their functions usually occur within the chapters on sensation. There are brief descriptions of the receptor organs patterned usually after Ewald; together with an account of how the inertia of the liquid within the canals sets the end-organs into function. The writers disagree, however, concerning the kind of mental events aroused. Ladd and Woodworth (*931*, p. 211) suggest that the "swimming sensation of the head which accompanies dizziness is probably to be ascribed to the semicircular canals." Later (p. 350) they speak of "a class of sensations which may be named labyrinthic" although "it is not possible as yet to say much regarding the sensory qualities belonging to the labyrinthic sense." Angell (*53*, p. 119) likewise speaks of "sensations of dizziness." Titchener (*1536a*, p. 174) describes the facts thus: "If you turn round rapidly upon the heels several times in succession, and then come to rest with closed eyes, you have a sensation which can only be described as a swimming in the head. . . . This swimming sensation which with practice may be observed to follow a quick movement of the head in any direction, comes from the cristae of the semicircular canals. At high intensities, it passes into dizziness or vertigo." Again (pp. 178, 180) he speaks of the "sensation of dizziness" and of sensations appearing as a "compression or lightness in the head." More recently (*1537*) he described definitely "the sensation of 'swimming' when the head is sharply jerked, and the sensation of *dizziness* when we twirl on our heels." Warren (*1611*) likewise urges the existence of a unique element. For example, "the stimuli for sensation of the static sense are alterations in pressure of the endolymph. . . . The static sense gives sensations of *position* and sensation of *motion*. In both cases the static sensation is so

closely bound up with muscle sensations and other kinaesthetic data that it is difficult to distinguish its own particular quality. The sensation of motion apparently differs in quality from the sensation of position. . . . The sensations from the three semicircular canals may also differ in quality. . . ."[66]

Pillsbury (*1237*) is not sure whether excitations of the vestibular end-organs give rise to sensations of their own or not. He gives his reasons for believing that "the sensation of giddiness is not a true sensation of the vestibular nerve, but rather a sensation from the alimentary canal, due to reflexes excited by the organs of equilibrium. . . . The sensations arise from the reflexes when they become intense." More recently (*1238*) he says: "It is, perhaps, a question whether the static sense is a real sense, for we become aware of its action only indirectly through the movements it induces or, when the excitation is more intense, by the disturbances of the alimentary tract that give rise to sensations of giddiness. Külpe (*924*, pp. 151, 152) likewise doubts a specific mental element. "The only psychological process which appears to represent the activity of the organ in consciousness is that of *giddiness*; . . . but it is difficult to say what the common element in sensations of giddiness is, when we have abstracted from the objective disturbance of the co-ordination of movements and its various concomitant phenomena." Later on (p. 378) he observes that "the position of the body is inferred, when the eyes are closed, simply from cutaneous and articular sensations." Wundt (*1683*, v. ii., p. 507) has also questioned the existence of special sensory qualities from the canals, since deaf and dumb subjects acquire "mit Hilfe anderer Sinne, namentlich des Tast-und Gesichtssinnes, eine so vollständige Orientierungsfähigkeit im Raume, dass er, so schwer er den Mangel des Gehörs empfinden mag, den dieses Orientierungsorgans kaum zu bemerken scheint. . . . Ein Organ, das in solcher Weise durch andere vertreten wird, kann aber keine spezifische, nur ihm eigentümliche Funktion haben." Wundt finds, however, that the "tonische Organ" is functionally related to the other senses. These facts led him to conclude that "der tonische Sinn kein für sich isolierbares Vorstelungsgebiet umfasst, da er niemals für sich allein Wahrnehmungen des Gleichgewichts und der Bewegungen des Körpers oder gar des Raumes in allgemeinen vollziehen

[66]Warren here likens these differences to the local signs found in the sense of touch. He seems here to have been strongly influenced by Cyon.

kann, ähnlich wie ja selbst der Sehende niemals durch den blossen Tastsinn Wahrnehmungen äusserer bestaterer Objekte gewinnt, bei denen nicht, auch ohne er es will, Assoziationen mit den Vorstellungen des Gesichtssinnes mitwirken." The semicircular canals are then, for him "a kind of inner organ of touch" (p. 508).

As a result of repeated rotations covering long periods of time Griffith (*689*) came to the conclusion that there was no unique mental quality attributable to the canals. To quote: "We have found the experience of dizziness or vertigo to be made up of a large number of processes the most prominent of which are (1) kinaesthesis from the eyes and neck and in the arms, (2) pressure from the region of the abdominal viscera, the chest and head, and (3) certain vascular processes which supply an obscure background and which give to the whole experience a characteristic shading" (*op. cit.* pp. 124-125). Griffith found, moreover, that the whole experience of dizziness becomes less complex and less intensive under periodic repetition. It even becomes possible to arrive at a condition in which none of these processes arise. That is to say, the whole perception of rotation comes to be carried in terms of accessory processes.

3. *Summary and conclusion.* There has been, then, no serious attempt on the part of psychologists to get behind the "stimulus error" and to take account (a) of the mental processes actually found in mind during and after rotation; and (b) of the presence or absence of an element unique in the experience of rotation. Such descriptions as have been given, come, for the greater part, as the logical result of theories about the canals and their functions and not from an accurate and painstaking analysis of the experience of rotation itself.

III

GENERAL SUMMARY AND CONCLUSION

WE have come now to the end of this historical survey. It has presented us with the following facts. (a) Only a part of the inner ear is concerned solely with hearing. The remainder, *-viz.*, the semicircular canals and the utriculus and sacculus,-seems to be very closely connected with the maintenance of bodily equilibrium. (b) The structure of the end-organs in the ampullae and in the vestibular enlargements is such as strongly to suggest such a function. Furthermore, differences in the structural complexity of these end-organs among the vertebrates and corresponding differences in equilibratory ability are striking. (c) The theory that actual movements occur in the liquid in the canals or in the ampullae has little in its favor but small changes of pressure may occur in the system in such a way as to excite the delicate endings of the vestibular branch of the VIIIth nerve. Conclusive evidence regarding the mode of operation of the end-organ has apparently not been secured. (d) There is evidence that the excitation of the equilibratory end-organs affects the ability of an organism to maintain its position. By means of these organs the body becomes sensitive to changes in either translational or rotational movements. Frequently the organism makes a variety of compensatory movements to such displacements of its position. (e) Histology has demonstrated that the cerebellum is, in a sense, a suprasegmental development of the vestibular nucleus of the VIIIth nerve, a fact which strengthens the belief that the end-organs in the canals are closely related to motor control. Other central connections are, however, but imperfectly understood. (f) The apparent demonstration that the canals are phylogenetically related to the lateral line canals and that the latter are probably equilibratory organs gives a genetic warrant for the assumption that the canals bear a similar function. (g) A great deal of pathological evidence from the clinical laboratory testifies still more directly to the equilibratory functions of the end-organs in the canals or in the vestibular enlargements.

In brief, the location of the canals in the cephalic end of the

organism, their general form and structure, their relation to the lateral line canals, their central connections, their mode of excitation, and the results of pathological affections, all indicate that the end-organs within the canals are admirably adapted for the purpose of maintaining the equilibrium of the body. The facts do not show, however, that they are the sole organs. On the mental side, there is no reason to suppose that they directly furnish even the necessary sensory materials for the perception of rotation or of other movements. Nevertheless, they have come to be regarded in certain quarters as the sole means of bodily equilibration. Adequate reasons for this intemperate view are not wanting. In the first place, the whole experimental history of vestibular functions has concerned itself, as we have seen, with the immediate effects of excitation and not with continued or repeated excitations. This limitation of method rests, in part, upon the use of surgical means of exciting the canals, and, in part, upon the fact that the ocular effects have been given undue attention because of their regularity in appearance and the ease with which they can be controlled. These facts, taken together with a naive application of the principle of inertia to the liquid in the canals and a theoretical account of the central connections, have recently led to questionable views in clinical otology. In contrast to the clinical description of the vestibular functions, recent investigations have shown that the ocular movements are not simple reflexes, that there is no such mental element as 'vertigo,' and that the whole group of effects issuing from vestibular excitation must be considered, not as unrelated responses, due in part to cortical and in part to subcortical mechanisms, but as a highly integrated and coordinated totality.

IV

A BIBLIOGRAPHY OF EQUILIBRATION

THE problems of equilibration have given rise, as we have seen, to a compendious experimental literature. Up to the present time, the larger part of this literature is from the physiological laboratory; but the problem is so obviously mental that the next few years ought to see a vigorous attack in the psychological laboratory upon such experiences as 'dizziness' and 'vertigo.' In the preceding sections the writer has endeavored to show where the significant physiological and psychological problems lie and he has, moreover, sought to provide a background for further analytic work. This purpose can be further served by an exhausive bibliography of the literature dealing with the equilibratory functions. The following bibliography includes, it is believed, a very large proportion of the German, French, and English titles on the normal equilibratory functions up to and including the year 1920. The writer has been unable to get at all of the Russian, Scandinavian, and Italian titles; although many of them are included. None save the most significant and illustrative pathological titles have been included. Owing to the notable increase of interest in the vestibular functions since Bàràny's work, the medical journals are full of 'case-descriptions.' Such titles have, for the most part, been omitted. A few additional titles on related topics will be found, especially such as append their own bibliographies.

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V.

THE CHRONOLOGICAL DISTRIBUTION OF THE TITLES

TO assort by number the titles that have just been listed in temporal periods constitutes in itself a short history of equilibration. The distribution is, however, to be taken for what it suggests and not as a reliable index of temporal sequence. Although every effort has been made to search out every published paper, some have been missed and the difference in accessibility has probably made the list in recent years the more complete. The writer does not feel, however, that this error in distribution can be very great. Since no attempt has been made to include all of the clinical and pathological titles, the list is not weighted so heavily at the end as it might otherwise be. The titles appearing prior to 1820 are but secondary in interest, a fact that can be substantiated by appealing first of all to the tabular distribution given below and by turning then to the bibliography itself. It will be observed that, in this period, the titles appear at wide intervals and that they deal mostly with general problems of physiology and of audition. Two or three studies on galvanic vertigo and upon neurology presage the coming interest in the equilibratory mechanisms.

Purkinje's study (*1257*) on vertigo appeared in 1820 and Flourens' first experiments on the pigeon in 1824 (*599*). From that time, the problems took definite form with significant studies by Aubert (*61*), Purkinje (*1258*, *1259*), Chevreul (*407*), Flourens (*600*, *601*), Romberg (*1320*), and others. By 1865, the problem was gaining momentum, 23 titles appearing between 1865 and 1869. Within the next three decades, studies on all phases of the problem accumulated rapidly. Mach, Breuer and Crum Brown published their studies on the mode of excitation of the receptor in 1874 and from then until 1900 the problem was worked out in the physiological laboratories. Beginning with 1900, the character of the titles changes. Studies of a purely experimental nature begin to give way to clinical

studies and within recent years most of the literature has come from the pathological laboratory.

The chronological distribution of the titles is as follows:

Year	Title Number
1575–1579	*1081.* Total: 1.
1680–1684	*542.* Total: 1.
1730–1734	*543.* Total: 1.
1735–1739	*544.* Total: 1.
1775–1779	*651, 1107.* Total: 2.
1780–1784	*363.* Total: 1.
1790–1794	*760.* Total: 1.
1795–1799	*488, 761.* Total: 2.
1800–1804	*63, 64, 1150.* Total: 3.
1805–1809	*452, 1315.* Total: 2.
1810–1814	*703.* Total: 1.
1820–1824	*599, 1257.* Total: 2.
1825–1829	*61, 302, 1106, 1258, 1259, 1520.* Total: 6.
1830–1834	*399, 407, 600, 601, 1320.* Total: 5.
1835–1839	*310, 451, 1499, 1547.* Total: 4.
1840–1844	*586, 602, 708, 806, 863, 1151.* Total: 6.
1845–1849	*724, 807, 1168, 1247.* Total: 4.
1850–1854	*325, 331, 431, 692, 1540, 1629.* Total: 6.
1855–1859	*208, 820, 1375.* Total: 3.
1860–1864	*58, 332, 480, 497, 603, 728, 851, 1110, 1260, 1295, 1600.* Total: 11.
1865–1869	*47, 198, 290, 309, 397, 730, 731, 743, 749, 983, 997, 1048, 1053, 1115, 1163, 1185, 1337, 1338, 1339, 1480, 1541, 1604, 1612.* Total: 23.
1870–1874	*213, 237, 245, 291, 292, 311, 312, 313, 329, 348, 357, 439, 440, 441, 450, 572, 667, 668, 732, 768, 769, 770, 771, 862, 877, 995, 996, 1006, 1007, 1015, 1034, 1126, 1189, 1246, 1261, 1263, 1340, 1384, 1385, 1393, 1431, 1434, 1501.* Total: 43.
1875–1879	*199, 209, 239, 244, 249, 253, 285, 286, 287, 293, 314, 437, 442, 454, 455, 456, 457, 458, 481, 482, 516, 528, 530, 647, 672, 676, 714, 750, 754, 755, 785, 818, 920, 921, 945, 994, 1016, 1047, 1096, 1113, 1114, 1132, 1147, 1181, 1221, 1256, 1300, 1394, 1396, 1442, 1450, 1451, 1452, 1538, 1550, 1554, 1555, 1579, 1614, 1615, 1660.* Total: 61.

1880–1884 *44, 83, 84, 85, 86, 166, 170, 171, 172, 173, 174, 175, 204, 254, 333, 353, 359, 442a, 484, 541, 786, 787, 788, 789, 798, 808, 810, 819, 822, 864, 865, 922, 923, 928, 998, 999, 1097, 1098, 1131, 1179, 1184, 1205, 1222, 1223, 1243, 1301, 1376, 1406, 1441, 1443, 1444, 1571, 1588, 1601, 1605, 1616, 1628, 1661.* Total: 58.

1885–1889 *49, 56, 59, 60, 62, 87, 88, 167, 168, 176, 315, 335a, 336 443, 444, 445, 453, 459, 499, 500, 501, 502, 503, 504, 511, 546, 553, 554, 557, 558, 559, 648, 665, 693, 812, 852, 853, 879, 880, 893, 894, 895, 988, 1000, 1120, 1149, 1250, 1341, 1369, 1391, 1392, 1478, 1479, 1481, 1482, 1483, 1498, 1533, 1589.* Total: 59.

1890–1894 *45, 65, 66, 81, 82, 177, 188, 210, 214, 235, 257, 258, 259, 260, 303, 316, 334, 358, 382, 422, 427, 433, 560, 561, 562, 563, 564, 573, 574, 577, 578, 579, 580, 581, 585, 598, 634, 655, 670, 718, 751, 801, 802, 846, 854, 896, 898, 903, 904, 905, 906, 908, 911, 942, 956, 957, 958, 985, 989, 990, 1001, 1002, 1003, 1008, 1031, 1060, 1082, 1083, 1111, 1128, 1158, 1159, 1177, 1244, 1276, 1312, 1344, 1370, 1371, 1372, 1373, 1374, 1377, 1427, 1445, 1457, 1458, 1459, 1495, 1585, 1617, 1618, 1658, 1659, 1681.* Total: 95.

1895–1899 *10, 11, 178, 179, 189, 190, 191, 211, 215, 216, 217, 218, 221, 226, 261, 262, 263, 264, 265, 266, 267, 268, 269, 317, 318, 319, 324, 335, 339, 349, 352, 394, 401, 412, 413, 414, 415, 416, 446, 447, 460, 461, 462, 463, 492, 505, 515a, 526, 549, 550, 551, 565, 566, 567, 568, 569, 570, 608, 633, 636, 637, 642, 646, 662, 669, 715, 735, 736, 747, 752, 756, 758, 765, 823, 824, 826, 827, 828, 856, 890, 891, 909, 924, 927, 947, 948, 949, 959, 1005, 1011, 1012, 1017, 1018, 1019, 1076, 1084, 1085, 1086, 1112, 1129, 1141, 1155, 1164, 1165, 1169, 1170, 1183, 1215, 1277, 1282, 1303, 1304, 1342, 1378, 1460, 1491, 1492, 1493, 1494, 1513, 1514, 1515, 1528, 1529, 1530, 1531, 1549, 1566, 1572, 1573, 1586, 1610, 1624, 1626, 1672, 1682.* Total: 136.

1900–1904 *4, 5, 6, 7, 8, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 37, 38, 39, 40, 41, 46, 50, 54, 72, 73, 89, 94, 155, 197, 206, 227, 228, 230, 233, 236, 270, 271, 272, 273, 274, 275, 276,*

277, 278, 279, 280, 281, 294, 295, 300, 301, 320, 321, 408, 409, 410, 411, 420, 430, 434, 435, 436, 464, 465, 466, 467, 468, 469, 470, 471, 472, 473, 474, 491a, 506, 507, 508, 509, 510, 514, 517, 522, 523, 525, 532, 534, 552, 583, 606, 612, 614, 615, 625, 629, 630, 631, 638, 639, 640, 645, 653, 654, 656, 683, 684, 717, 722, 725, 727, 748, 759, 772, 778, 780a, 781, 790, 791, 793, 813, 814, 815, 816, 825, 850, 868, 874, 875, 892, 897, 899, 912, 918, 937, 938, 943, 944, 950, 951, 974, 975, 1004, 1013, 1020, 1055, 1056, 1057, 1062, 1063, 1064, 1065, 1121, 1133, 1134, 1135, 1152, 1153, 1182, 1187, 1191, 1193, 1194, 1195, 1196, 1197, 1198, 1199, 1200, 1206, 1249, 1254, 1255, 1265, 1271, 1272, 1283, 1284, 1285, 1286, 1334, 1335, 1360, 1361, 1362, 1363, 1364, 1365, 1368a, 1389, 1395, 1401, 1402, 1404, 1405, 1409, 1422, 1429, 1430, 1449, 1453, 1461, 1462, 1463, 1464, 1465, 1466, 1467, 1468, 1469, 1470, 1471, 1472, 1473, 1474, 1485, 1496, 1497, 1517, 1524, 1527, 1532, 1556, 1564, 1567, 1568, 1574, 1581, 1582, 1587, 1593, 1609, 1625, 1651, 1673, 1675, 1680, 1684, 1686, 1694, 1696, 1699, 1700. Total: 242.

1905–1909 1, 2, 23, 24, 34, 36, 42, 43, 48, 53, 91, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 145, 161, 169, 180, 184, 194, 195, 196, 203, 207, 219, 220, 222, 223, 224, 229, 231, 232, 255, 282, 283, 288, 296, 297, 322, 323, 327, 330, 361, 364, 381, 383, 384, 398, 403, 405, 417, 421, 426, 428, 449, 475, 476, 477, 478, 489, 490, 493, 494, 495, 513, 524, 533, 540, 555, 571, 575, 576, 584, 596, 616, 617, 618, 619, 620, 632, 650, 671, 673, 686, 687, 688, 689, 690, 702, 705, 709, 716, 726, 738, 739, 753, 762, 766, 782, 784, 795, 796, 803, 821, 844, 855, 867, 885, 887, 888, 910, 914, 915, 916, 917, 925, 934, 953, 963, 967, 991, 993, 1009, 1021, 1023, 1024, 1025, 1026, 1035, 1050, 1051, 1059, 1066, 1067, 1069, 1070, 1077, 1088, 1099, 1100, 1101, 1102, 1108, 1119, 1124, 1130, 1137, 1139, 1142, 1148, 1154, 1156, 1166, 1167, 1171, 1176, 1192, 1201, 1202, 1207, 1210, 1212, 1213, 1217, 1219, 1224, 1230, 1234, 1235, 1236, 1262, 1266, 1273, 1274, 1279, 1290, 1302, 1314, 1327, 1333, 1345, 1346, 1349, 1350, 1357, 1358, 1359, 1366, 1387, 1388, 1397, 1398, 1407, 1410, 1411, 1423, 1424, 1425, 1437, 1438,

1439, 1440, 1448, 1475, 1476, 1484, 1486, 1504, 1505, 1506, 1507, 1518, 1521, 1522, 1539, 1542, 1543, 1544, 1545, 1546, 1553, 1562, 1563, 1565, 1575, 1576, 1583, 1594, 1595, 1596, 1597, 1598, 1599, 1602, 1603, 1643, 1644, 1645, 1647, 1649, 1652, 1653, 1654, 1664, 1665, 1666, 1667, 1668, 1677, 1683, 1865, 1687, 1688, 1701. Total: 265.

1910–1914 *25, 26, 27, 28, 29, 30, 31, 67, 68, 74, 75, 76, 77, 78, 79, 80, 92, 93, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133, 134, 135, 136, 137, 138, 139, 140, 143, 144, 146, 154, 156, 157, 158, 159, 160, 162, 163, 181, 182, 182, 183, 185, 186, 187, 192, 200, 201, 212, 240, 241, 242, 248, 284, 298, 305, 307, 340, 342, 344, 345, 346, 347, 354, 355, 356, 362, 365, 366, 367, 368, 369, 370, 371, 372, 373, 374, 375, 377, 378, 379, 380, 385, 386, 387, 388, 389, 390, 391, 392, 438, 479, 483, 486, 491, 496, 515, 519, 520, 529, 545, 556, 571a, 582, 597, 604, 609, 613, 621, 622, 627, 635, 657, 658, 659, 660, 661, 663, 664, 666, 679, 680, 681, 700, 704, 706, 710, 711, 720, 721, 733, 741, 763, 764, 767, 773, 774, 775, 776, 777, 783, 792, 797, 804, 805, 811, 845, 847, 848, 849, 861, 870, 871, 878, 881, 886, 889, 926, 931, 935, 936, 939, 940, 954, 955, 964, 965, 966, 969, 971, 976, 977, 978, 1014, 1032, 1036, 1037, 1040, 1041, 1042, 1043, 1045, 1046, 1049, 1052, 1058, 1071, 1072, 1073, 1074, 1078, 1079, 1089, 1090, 1091, 1103, 1105, 1122, 1123, 1127, 1140, 1143, 1145, 1146, 1157, 1172, 1173, 1175, 1180, 1188, 1190, 1203, 1208, 1211, 1214, 1226, 1239, 1242, 1245, 1253, 1267, 1281, 1287, 1289, 1291, 1292, 1293, 1296, 1297, 1298, 1305, 1306, 1311, 1317, 1322, 1233, 1324, 1325, 1326, 1328, 1329, 1331, 1332, 1336, 1347, 1351, 1352, 1353, 1354, 1368, 1380, 1386, 1390, 1399, 1400, 1408, 1412, 1413, 1414, 1415, 1416, 1417, 1418, 1428, 1433, 1435, 1436, 1446, 1455, 1477, 1487, 1488, 1489, 1508, 1523, 1526, 1535, 1536, 1569, 1570, 1577, 1578, 1592, 1608, 1613, 1619, 1621, 1626a, 1627, 1631, 1633, 1634, 1635, 1636, 1637, 1638, 1639, 1648, 1655, 1656, 1689, 1691, 1692, 1693, 1698.* Total: 326.

1915–1919 *3, 32, 33, 35, 52, 55, 70, 71, 141, 142, 147, 148, 149, 150, 151, 152, 164, 193, 202, 205, 234, 238, 243, 246, 250, 251, 252, 299, 328, 341, 343, 350, 351, 360, 395, 404, 406, 418, 423, 432, 448, 485, 521, 527, 531, 536, 538, 539, 588, 589, 590, 591, 592, 593, 594, 605, 611, 623, 624, 628, 643, 652, 674, 675, 677, 678, 682, 691, 701, 707, 712, 713, 734, 740, 742, 744, 745, 757, 779, 817, 830, 831, 835, 836, 837, 838, 839, 840, 841, 842, 843, 859, 860, 876, 882, 883, 913, 929, 930, 941, 968, 970, 972, 979, 980, 981, 984, 1027, 1028, 1029, 1030, 1038, 1039, 1044, 1054, 1080, 1092, 1104, 1117, 1118, 1125, 1138, 1160, 1161, 1162, 1178, 1204, 1109, 1216, 1218, 1220, 1227, 1228, 1229, 1229a, 1233, 1237, 1248, 1251, 1252, 1268, 1269, 1278, 1294, 1299, 1307, 1308, 1309, 1310, 1316, 1318, 1319, 1355, 1356, 1367, 1379, 1381, 1382, 1419, 1420, 1421, 1426, 1432, 1447, 1490, 1500, 1503, 1509, 1510, 1511, 1512, 1516, 1534, 1537, 1548, 1552, 1557, 1558, 1559, 1560, 1584, 1611, 1622, 1623, 1630, 1632, 1640, 1641, 1642, 1646, 1663, 1678, 1679, 1690, 1695.* Total: 195.

1920–1921 *9, 247, 289, 326, 376, 393, 396, 537, 595, 644, 649, 694, 695, 696, 697, 698, 699, 729, 799, 800, 829, 866, 872, 873, 884, 982, 986, 992, 1068, 1087, 1093, 1094, 1095, 1238, 1240, 1270, 1321, 1343, 1383, 1454, 1519, 1591, 1662.* Total: 43.